

Canada, F. R. B. Journal		PERIODIC
V. 18		
1960		
Volume & DATE OF MAGAZINE	BORROWER'S NAME	
18(6) December	R. L. Hill	
JUN 28 1962	Seepel	
12/16/68	SEP	

PERIODICAL
CANADA.
F. R. B.
JOURNAL

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JOURNAL
OF THE
FISHERIES RESEARCH BOARD
OF CANADA

Volume 18

1961

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QUEEN'S PRINTER AND CONTROLLER OF STATIONERY
OTTAWA, 1961

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Zooplankton Studies at Ocean Weather Station "P" in the Northeast Pacific Ocean¹

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ABSTRACT

Concentrations of zooplankton observed at Station "P" (50° N.L., 145° W.L.) are less than those in the Northwest Pacific, the Bering Sea, British Columbia coastal waters and the Labrador Sea; about equal to those at Station "M" in the Norwegian Sea; and greater than those in the central Equatorial Pacific and the Sargasso Sea. Zooplankton abundance at Station "P" appears representative of that in a wide area of the central Gulf of Alaska. A vertical distribution of zooplankton characterized by maxima of concentration from 0–100 metres and from 200–500 m was observed both day and night and in all seasons. Daily means of concentration of surface zooplankton ranged from about 20 g per 1000 m³ in winter to about 150 in summer. A small autumn maximum was observed. A similar seasonal cycle of abundance occurred down to depths of about 200 m. Below 200 m the amplitude of the seasonal cycle tended to decrease with depth. Vertical hauls captured mainly copepods all year round. Horizontal surface tows revealed a marked seasonal cycle in taxonomic composition. A pronounced diurnal variation in the concentration of surface zooplankton was observed and showed the major features of typical diurnal vertical migration. Night catches of vertical hauls exceeded day catches.

A. INTRODUCTION

OCEAN WEATHER STATION "P" is located at Latitude 50° N, Longitude 145° W about 500 miles west of the north end of Vancouver Island (Fig. 1). The station is manned by two Canadian ships alternately, each occupying the position for 6 weeks, and being relieved on station by the other.

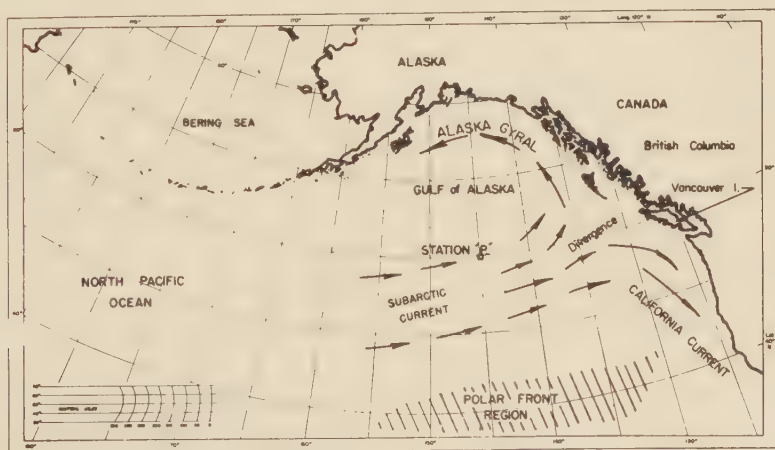


FIG. 1. Chart showing position of station "P".

¹Received for publication June 1, 1960.

Since 1952 bathythermograph lowerings have been made twice daily on station, and approximately every 30 miles en route to and from the station. In August 1956, the C.G.S. *St. Catharines* was equipped for carrying out a more detailed program of oceanographic observations. The data are published annually (Pacific Oceanographic Group, 1957b, 1958).

In the present study some of the major features of the zooplankton data obtained during the first year and a half of the detailed program are discussed.

B. INTRODUCTION TO THE PHYSICAL OCEANOGRAPHY

Station "P" lies within the subarctic water mass of the North Pacific Ocean (Sverdrup *et al.*, 1942). The subarctic water mass may be characterized by its vertical salinity structure (Fig. 2) which consists of 3 layers (Tully and Dodimead,

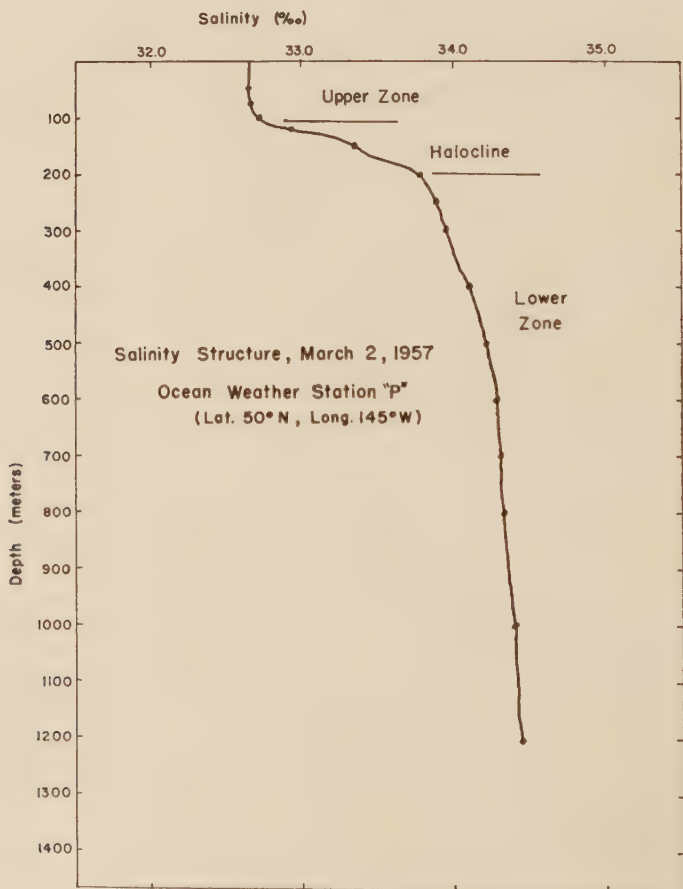


FIG. 2. Typical salinity structure in the subarctic water mass of the Northeast Pacific.

MS, 1957): an almost homogeneous upper layer having relatively low salinities; a permanent halocline with a salinity change of about 1‰ and which marks the limit of seasonal variation; and below 200 m, a deep zone in which salinity gradually increases with depth.

Doe (1955) described 3 oceanographic regions (Fig. 3) in the relatively homogeneous subarctic area of the Northeast Pacific: a continuous "coastal" region having surface salinities less than 32.5‰; an "offshore" region with surface salinities averaging about 32.6‰; and a "midgulf" region with higher salinities than the surrounding "offshore" water.

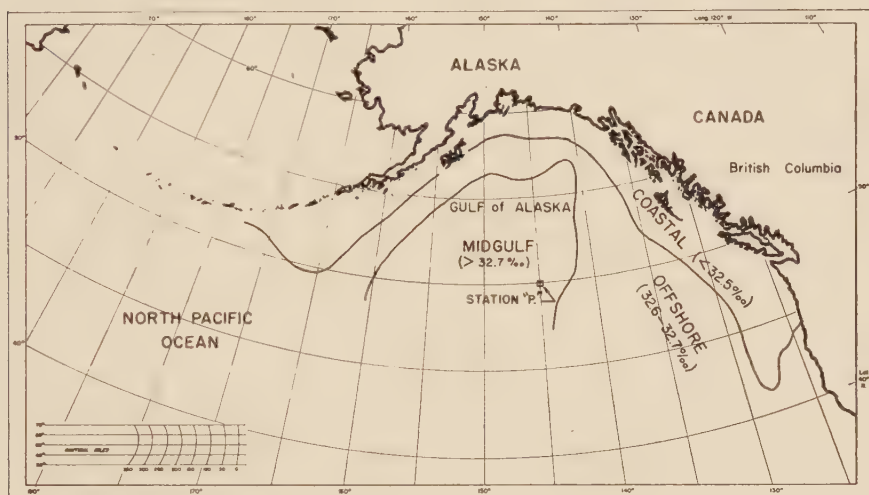


FIG. 3. Oceanographic regions in the Northeast Pacific (after Doe, 1955).

The three regions described by Doe (1955) can be identified in the plots of salinity data (Fig. 4) presented by Tully and Dodimead (1957) and Dodimead (1958). The "midgulf" water occupies the northwest part of the Gulf of Alaska and the low salinity "coastal" water lies along the British Columbia and Alaska coastline. The "offshore" region, with salinities of about 32.6‰, lies between the "midgulf" and "coastal" regions and is bounded on the south by the Polar Front (see below). Station "P" appears to occupy a position near the diffuse boundary between "midgulf" and "offshore" water.

Temperature-salinity relationships also suggest that station "P" lies near the boundary region between "midgulf" and "offshore" waters. The distribution of some of these relationships, as arbitrarily defined by Tully and Dodimead (1957), is presented in Fig. 5. Examination of the figure suggests that relationships 10 and 11 correspond to Doe's "midgulf" and "offshore" waters respectively.

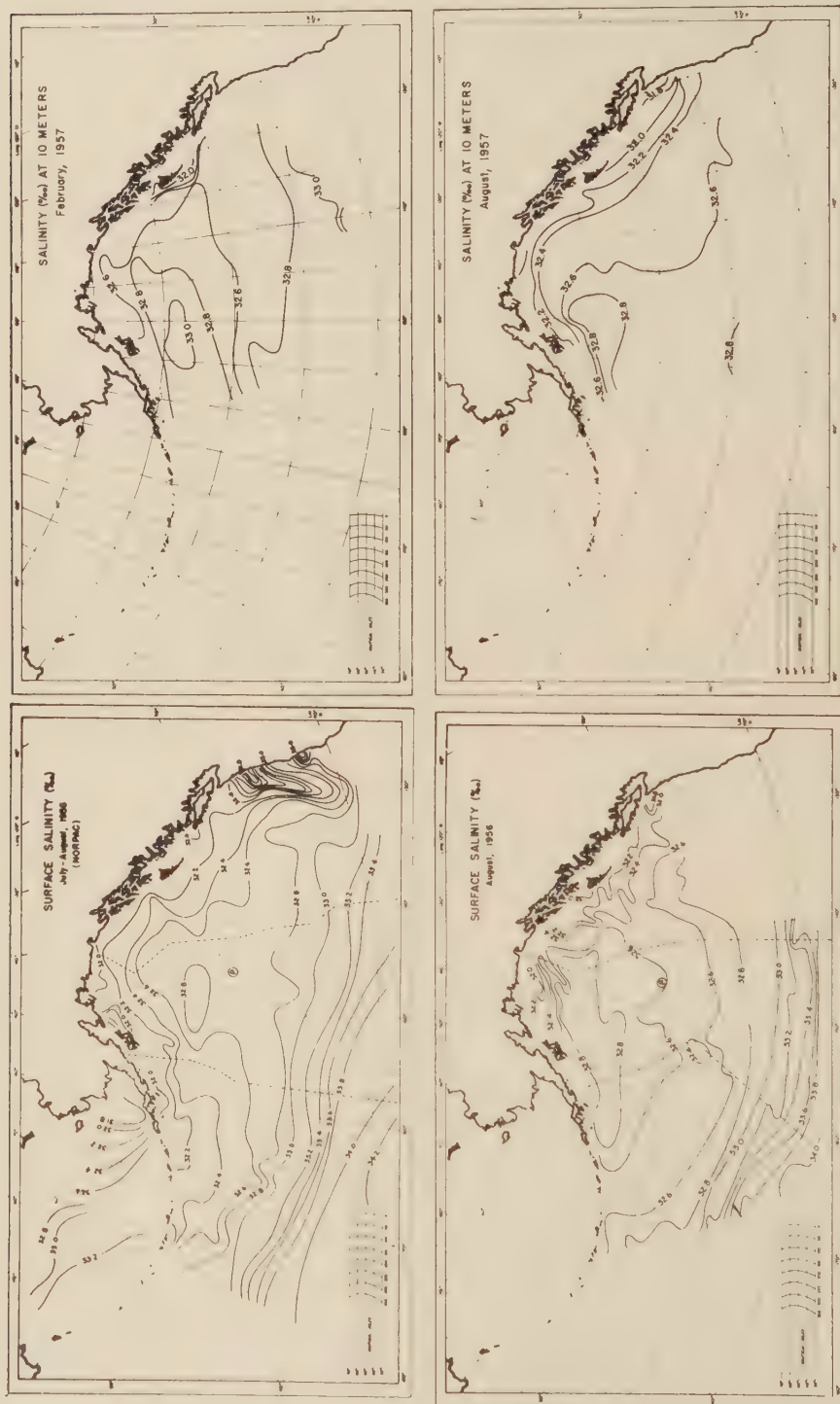


FIG. 4. Distributions of salinity in the Northeast Pacific (from Tully and Dodeimead, MS, 1957; and Dodeimead, MS, 1958).

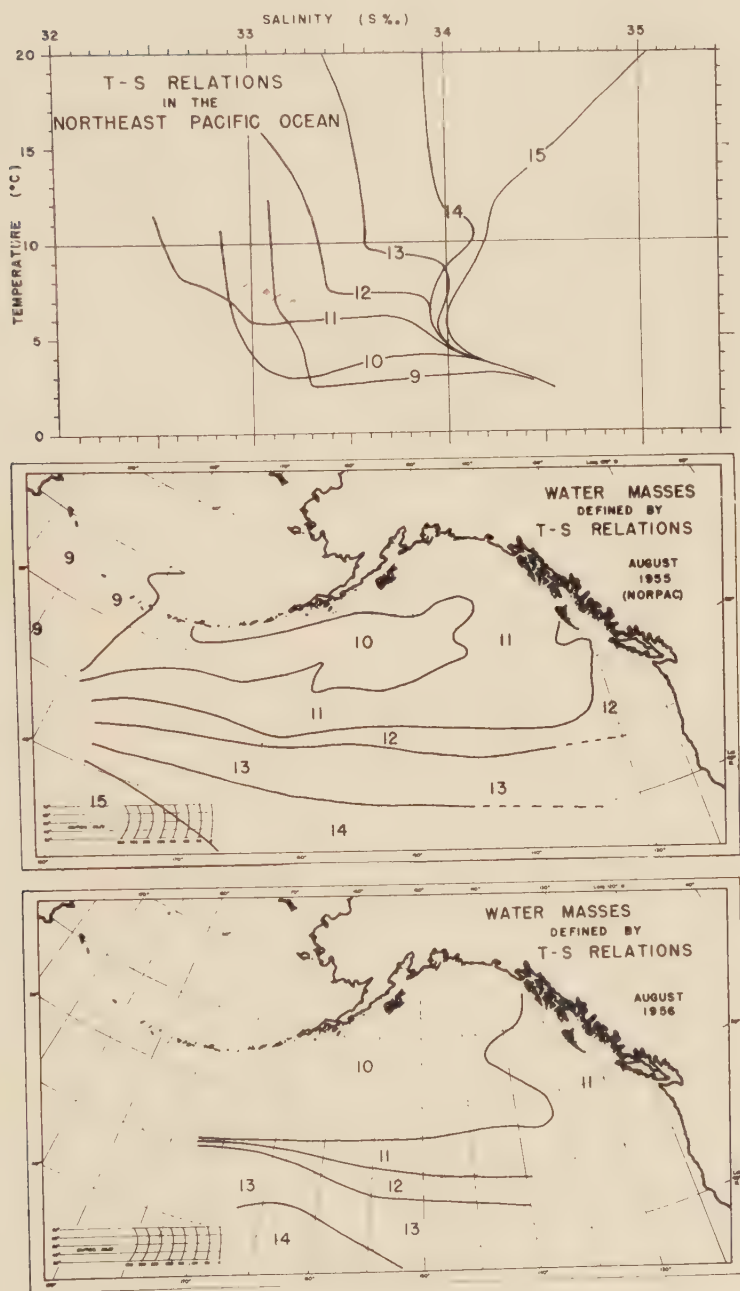


FIG. 5. Temperature-salinity relationships in the Northeast Pacific (From Tully and Dodimead, MS, 1957).

It can be seen in Fig. 6 that temperature-salinity relationships observed at station "P" are intermediate between these two types.

The Subarctic Current (Sverdrup *et al.*, 1942) enters the area surrounding station "P" from a westerly direction and diverges east of the station to from

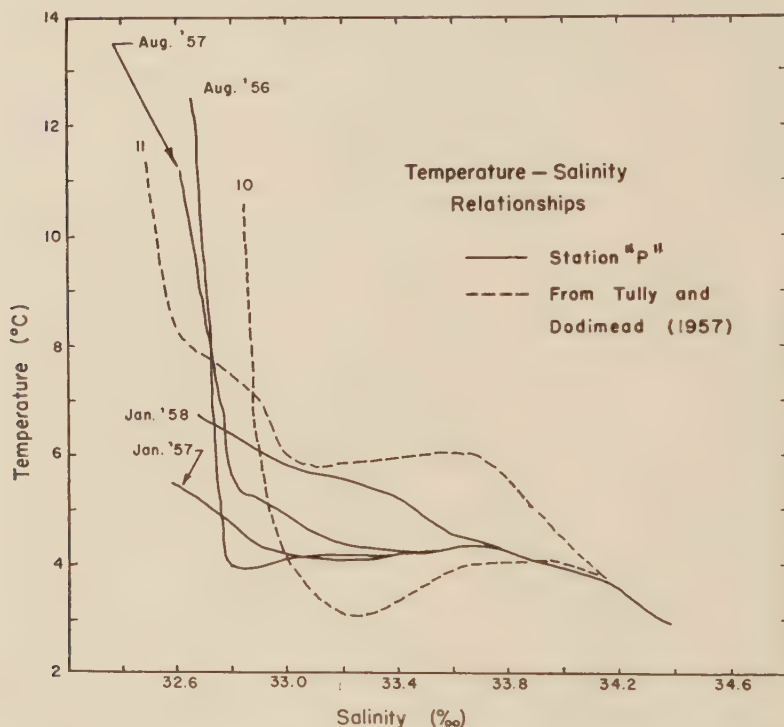


FIG. 6. Temperature-salinity relationships at station "P".

the south-flowing California Current and the counter-clockwise Alaska Gyral (Fig. 1). The currents near station "P" are slow, from 1 to 2 sea miles per day (Dodimead, 1958).

South of station "P" gradients of rising salinity (Fig. 4) and temperature (Fig. 7) increase to form the Polar Front (Fig. 1) (Tully and Dodimead, 1957).

In summary, station "P" might be considered to lie in an oceanographic area bounded on the northwest by the centre of the Alaska Gyral ("midgulf" water), by the coastal region to the northeast, by the divergence of the Subarctic Current to the east, and by the Polar Front to the south. Within this area, currents are sluggish and winter mixing is limited approximately to the upper 120 m of depth.

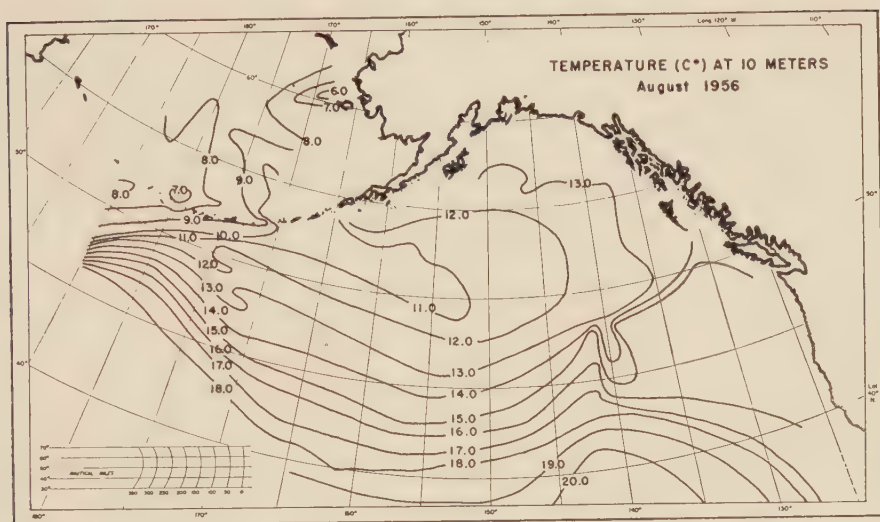


FIG. 7. Distribution of temperature in the Northeast Pacific (from Tully and Dodimead, MS, 1957).

C. METHODS

1. SAMPLING TECHNIQUES

The plankton samples studied here were obtained during alternate 6-week periods beginning August 26, 1956 and ending January 23, 1958. (Table I, Fig. 8).

All samples were taken with a standard "NorPac" net (Reid, 1956), 45 cm in diameter, 180 cm long, and made of nylon netting of 0.33 mm aperture width (equivalent to No. 3 silk bolting cloth).

Three series of observations were made:

1. Nets were hauled vertically from a depth of 150 m to the surface (August, 1956 to January, 1958).
2. Nets were towed horizontally at the surface, at 2-hour intervals, throughout 24-hour periods (December, 1956 to January, 1958).
3. Nets were hauled vertically from a series of depths (50, 100, 150, 200, 300, 500 and occasionally 1000 m) to the surface (March, 1957 to January, 1958).

The nets were not metered. However, the results of 150-metre vertical hauls from the Bering Sea (Hokkaido University, 1957) taken under similar operating conditions with metered "NorPac" nets, were used to estimate the efficiency of filtration. These data suggest that on the average the effect of the netting and clogging by organisms in reducing the amount of water entering the net is approximately balanced by the increase in the distance towed resulting

from ship's drift. An opening 45 cm in diameter will pass 24 m³ of water when hauled a distance of 150 m. The Bering Sea hauls filtered a mean volume of 25 ± 7 m³, close to the theoretical. It is therefore assumed that the nets used in vertical hauls at station "P" operated at 100% of nominal efficiency.

Horizontal surface tows were made at a speed of about 2 knots (1 m/sec) for 30 minutes. The net was towed with the opening approximately half submerged, thus reducing the ratio between the volume of water entering the net and the area of netting available for filtering. In calculating the results of surface tows the filtration was assumed to be 100% efficient.

2. TREATMENT OF SAMPLES

Fish and organisms exceeding $1\frac{1}{2}$ inches (38 mm) in length were removed from the samples before analysis. The percentage of the total wet weight formed by each major phylogenetic constituent was estimated by microscopic examination. Wet weights were determined after draining the samples in No. 20 silk bolting cloth (aperture 0.076 mm) and drying them for 10-15 minutes between layers of paper towelling. The percentages obtained from the microscopic examination were then used to calculate the weights of the constituents. The calculated weights of such forms as medusae, phytoplankton and detritus were subtracted from the total to give the weight of "edible" zooplankton. Concentrations are expressed in grams (wet weight) per 1000 m³ of water.

D. RESULTS AND DISCUSSION

1. LEVEL OF ABUNDANCE

Concentrations of zooplankton observed at station "P" ranged from about 0.3 to over 800 g per 1000 m³. Mean concentrations of zooplankton and their ranges are presented in Table I. The means were calculated from data presented in Fig. 8, 9, 10, 11, 12 and 13.

Zooplankton concentrations at station "P" are compared with those in other

TABLE I. Mean concentrations of zooplankton observed at ocean weather station "P" (Latitude 50° N, Longitude 145° W).

Type of sample	Sampling period	No. of samples	Mean concentration (g/1000 m ³)	Range (g/1000 m ³)
Surface tow	Dec. 56-Jan. 58	150	54	0-800
0-50 m vertical haul	Mar. 57-Jan. 58	27	48	7-327
0-100 m " "	Mar. 57-Jan. 58	27	48	1-294
0-150 m " "	Aug. 56-Aug. 57	61	31	0-200
0-150 m " "	Dec. 56-Dec. 57	69	29	0-200
0-200 m " "	Mar. 57-Jan. 58	27	37	3-215
0-300 m " "	Mar. 57-Jan. 58	27	39	8-136
0-500 m " "	Mar. 57-Jan. 58	26	40	6-118
0-1000 m " "	Apr. 57-Jan. 58	11	31	17-59

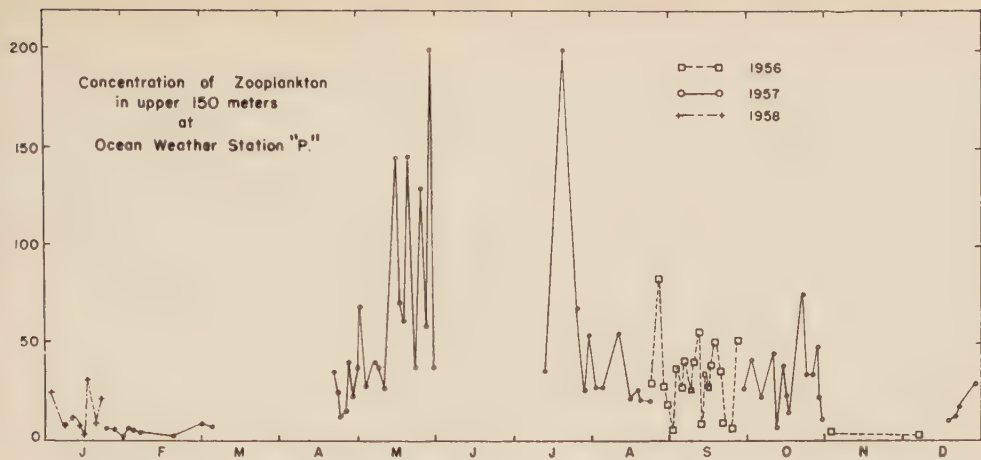


FIG. 8. Concentrations of zooplankton in the upper 150 m at Station "P".

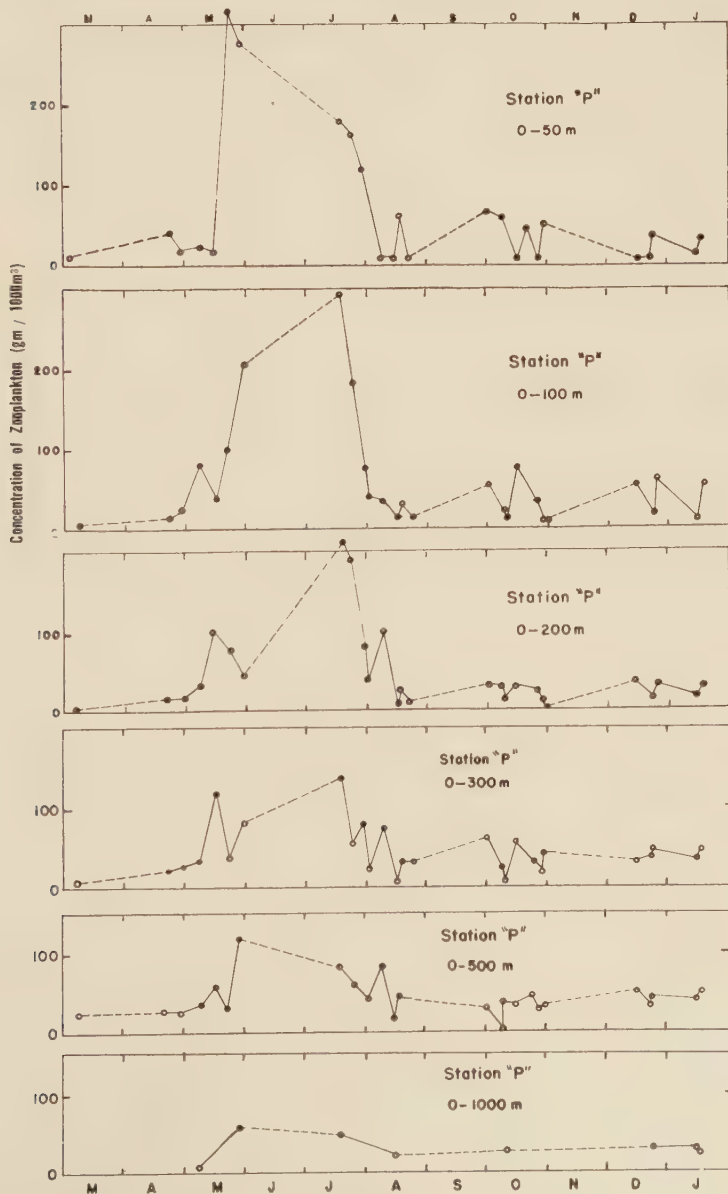


FIG. 9. Concentration of zooplankton from successive depths to the surface at Station "P".

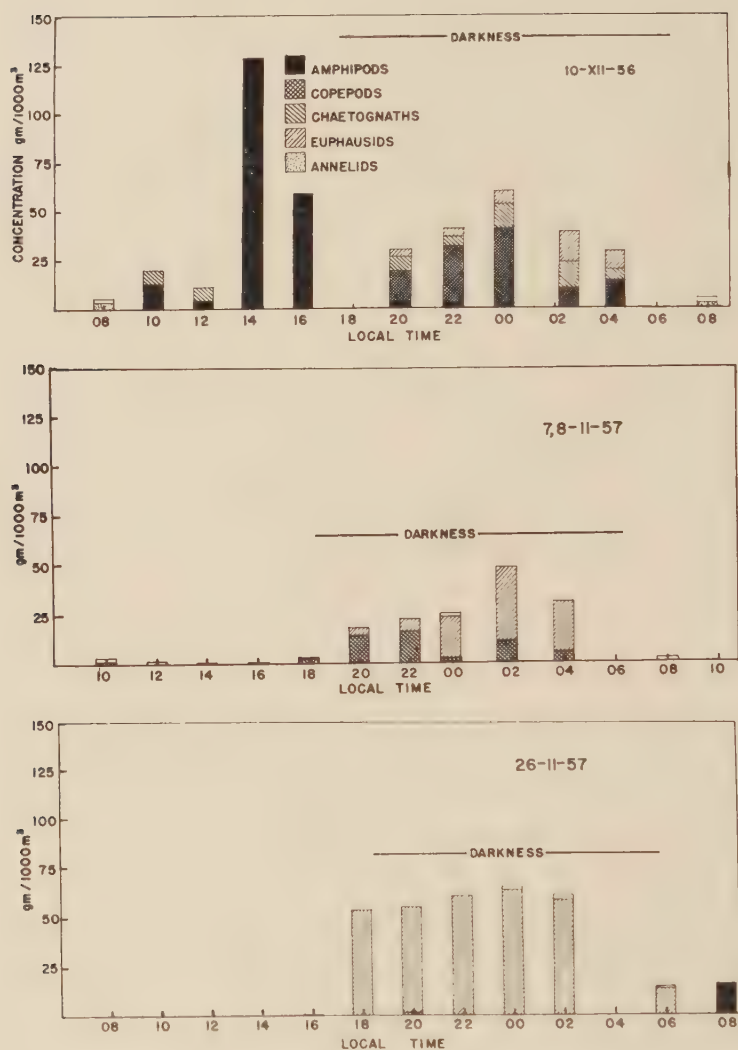


FIG. 10. The diurnal variation of surface zooplankton at station "P", Dec. 10, 1956, Feb. 7 and 8, 1957, and Feb. 26, 1957.

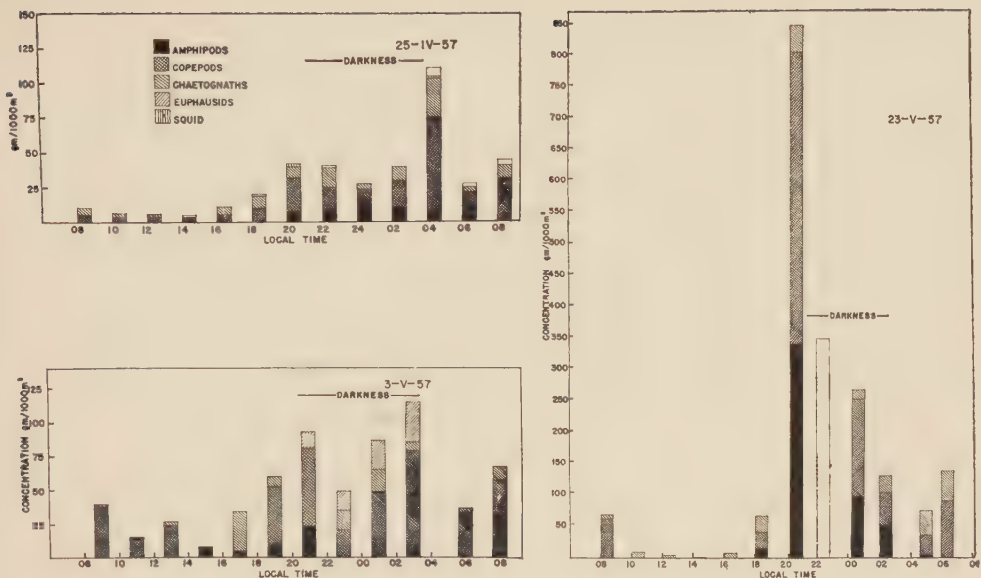


FIG. 11. The diurnal variation of surface zooplankton at station "P", April 25, 1957, May 3 and 23, 1957.

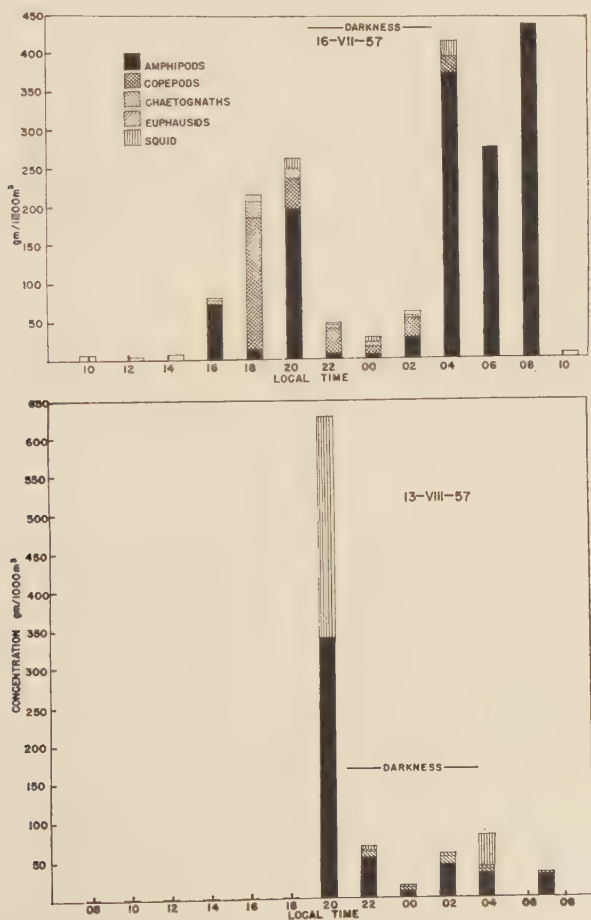


FIG. 12. The diurnal variation of surface zooplankton at station "P", July 16, 1957, and Aug. 13, 1957.

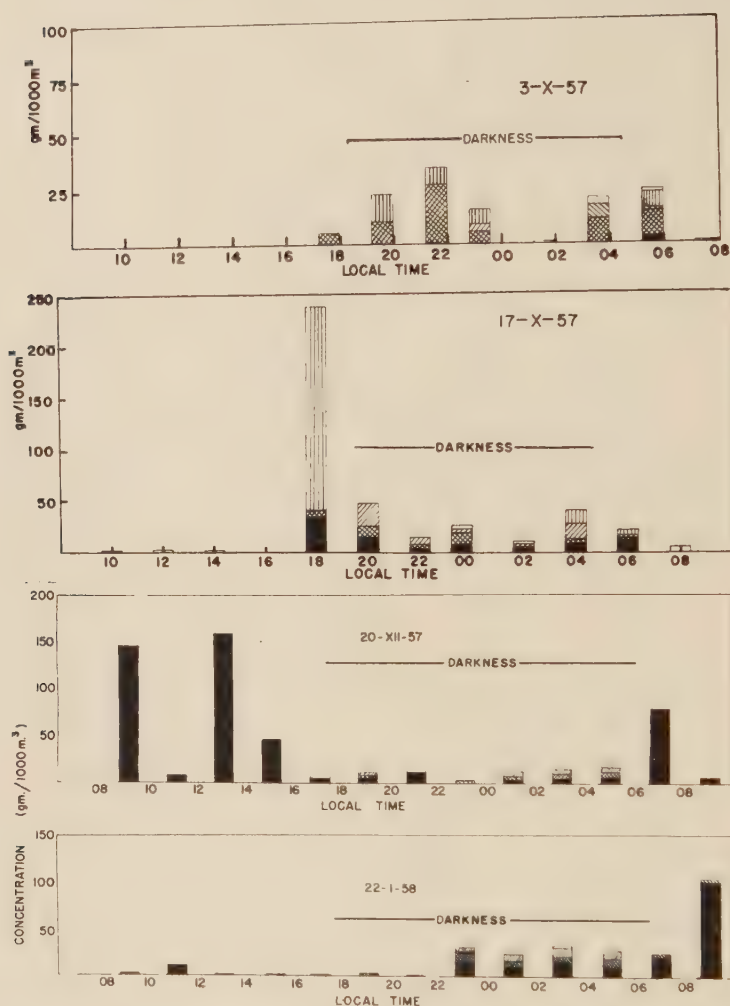


FIG. 13. The diurnal variation of surface zooplankton at station "P", Oct. 3 and 17, 1957, Dec. 20, 1957, and Jan. 22, 1958.

seas in Table II. The ratios can be only very approximate. Some of the data are separated by periods of years, were obtained with different nets and techniques, and recorded in different units. Concentrations expressed in terms of unit volume were multiplied by a factor of 0.62, determined from Bering Sea data (Hokkaido University, 1957), in order to obtain weights. Catches expressed in units per net haul were converted to weight per 1000 m³ of sea water by assuming that the nets operated at 100% efficiency.

According to the information in Table II, concentrations of zooplankton at station "P" are lower than those from the Northwest Pacific, the Bering Sea,

TABLE II. Comparison of zooplankton concentrations at ocean weather station "P" (Latitude 50° N, Longitude 145° W) with concentrations from other seas.

Sea area	Author	Date	Sampling method	Concentration (g/1000 m ³)	Conc. at "P" (g/1000 m ³)	Ratio Stn. "P" to other area
NW Pacific	Bogorov and Vinogradov, 1955	Summer	100 m vertical haul	100-500	12-294	0.12-0.59
Bering Sea	Hokkaido Univ. 1957	Aug. 1956	150 m vertical haul	200	42	0.21
Labrador Sea	Kielhorn, 1952	Annual	Surface (night)	342	85	0.25
B.C. Coast	P.O.G. unpublished	April, May 1957	150 m vertical haul	185	70	0.38
Norwegian Sea	Wiborg, 1954	Annual	100 m vertical haul	50	48	0.98
Central Equatorial Pacific	King and Hida, 1957	Annual	24-hour surface tows	35	54	1.54
Central Equatorial Pacific	King and Hida, 1957	Annual	200 m oblique haul	18	30	1.67
Sargasso Sea	Riley <i>et al.</i> , 1949	Annual	100 m vertical (Crustacea only)	17	40	2.35
Sargasso Sea	Fish, 1956	Annual	Surface (night)	10	85	8.5

the Labrador Sea, and British Columbia coastal waters; they are about equal to concentrations at ocean weather station "M" in the Norwegian Sea; and are greater than those from the central Equatorial Pacific and the Sargasso Sea.

The production of zooplankton is usually expected to be high in regions where physical processes tend to enrich the euphotic layer of the ocean with the nutrients necessary for the production of phytoplankton, the food of the zooplankton (Laevastu, 1957). Such regions may be found near areas of divergence between currents, along coasts where the action of wind-induced currents result in upwelling, and in the center of cyclonic gyral in the northern hemisphere. Areas in which currents and bottom configuration result in turbulence, and regions with intense winter overturn and mixing may also be productive.

Standing crops of zooplankton are also commonly found to be higher in or near such regions (Laevastu, 1957) but this need not be so, since areas of high production may have low standing crops of zooplankton if predation by fish is also high. High standing crops may also be found in regions where convergences, in the center of gyral or between currents, physically concentrate zooplankton (Laevastu, 1957).

At station "P" the currents are sluggish, the water is deep (approximately 4000 m), no strong convergences or divergences are present, the center of the nearest gyral is some 600 miles away and the stability imparted to the water column by the permanent halocline limits winter overturn and mixing to the upper 120 m. Thus, according to the physical criteria cited above, both the production and standing crop of zooplankton at station "P" should be relatively low. Although there are no data on production of zooplankton at station "P", the comparisons in Table II suggest that the standing crops are as might be expected.

The regions, shown in Table II, that have standing crops higher than those at station "P", all display one or more of the mechanisms described above as resulting in high production and standing crops of zooplankton. Convergences and winter overturn occur in the Northwest Pacific (Sverdrup *et al.*, 1942). The data from the Labrador Sea were obtained at ocean weather station "B", near the center of a large gyral and in an area with intense winter overturn (Kielhorn, 1952). Convergences (Laevastu, 1957), winter mixing, and bottom effects act in the Bering Sea. Along the British Columbia coastline wind-induced upwelling raises deep water to shallower levels (Doe, 1955).

However both the Norwegian Sea, with zooplankton concentrations about equal to those at station "P", and the central Equatorial Pacific, with less zooplankton than station "P", are also endowed with enriching physical mechanisms. Ocean weather station "M", at which the Norwegian Sea data were obtained, lies near the center of a gyral in a region where winter mixing is intense. Wiborg (1955) states that the Norwegian Sea is a productive region supporting rich

fisheries. The central Equatorial Pacific, with a marked divergence and convergence, is also believed to be a productive region (e.g., King and Hida, 1957). Since station "P" has standing crops of zooplankton equal to or greater than the above regions, it might be argued that "P" too, contrary to the earlier suggestion in this report, must lie in a productive region.

The contradiction may arise partly because of the difficulty of making valid comparisons amongst data not designed for the purpose. Also, the physical criteria used are incomplete and are valid only in a general way. The strength and duration of the enriching mechanisms, light intensities, effects of turbulence, rate of regeneration of nutrients, and other factors may also influence basic productivity, and hence production and standing crops of zooplankton. And it must be again emphasized that standing crops are determined by *consumption* as well as production. Direct measurements of basic production and of more members of the food chain are required.

Concentrations of zooplankton observed in the Northeast Pacific during recent oceanographic surveys are presented in Fig. 14. Mean concentrations of zooplankton observed at station "P" during periods coinciding with these oceanographic surveys are also entered in the figure. Because the data obtained during the several surveys in the summer of 1956 (Pacific Oceanographic Group, 1957a) were scattered in space and time they were combined by averaging the concentrations in "Squares" of 2.5° of latitude by 5° of longitude. However, because of the timing of the surveys and the distribution of stations this plot may include seasonal effects in spite of the averaging. The 1957 data (Pacific Oceanographic Group, 1957b, c) were obtained during two surveys of about 6 weeks' duration each, sufficient time for seasonal trends to occur (see Fig. 8). Short-term (Fig. 8) and diurnal (see below) variations complicate the distributions and the data are unevenly distributed around station "P". Thus, the contours entered on Fig. 14 are, at best, rough approximations.

However, it is tentatively concluded that concentrations of zooplankton at or near station "P" fall within the range of concentrations observed in that part of the Gulf of Alaska roughly coinciding with the diffuse boundary between "midgulf" and "offshore" water (Fig. 3, 5).

2. VERTICAL DISTRIBUTION

Vertical distributions of zooplankton at station "P" were calculated from the differences in catches of overlapping vertical hauls from successive depths to the surface. The results are summarized in Fig. 15 and 16.

The vertical distribution was usually characterized by two layers of maximum abundance separated by a layer of low abundance. The upper maximum occurred within the upper 150 m and was most often found within the upper 100 m, while the deeper maximum was on the average a broad one extending



FIG. 14. Some distributions of zooplankton in the Northeast Pacific.

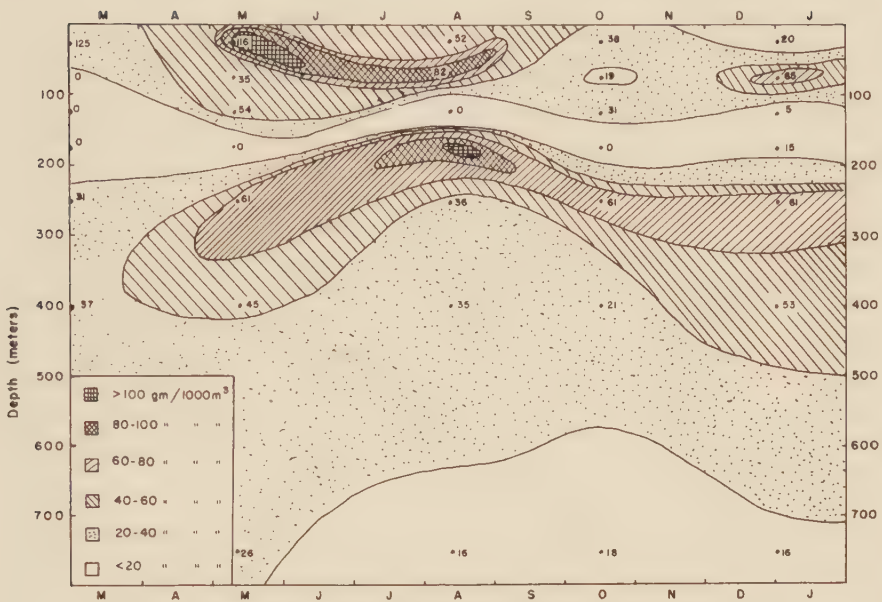


FIG. 15. The vertical distribution of zooplankton at station "P".

between depths of 200 and 500 m. The minimum layer between the two maxima occurred between depths of 50 and 300 m but was most often found between 100 and 200 m, tending to coincide with the depth of the permanent halocline.

In a similar vertical distribution observed in the Northwest Pacific by Brodsky (1955) the layer between the two maxima coincided with an intermediate core of cold water.

The deeper layer of zooplankton exists in a stratum too dark for phytoplankton production. In addition, the density gradient in the halocline might, to a large extent, prevent dead organisms and detritus from reaching the lower layer of zooplankton. Thus, in order to obtain sufficient food the herbivorous zooplankton in the lower layer may have to migrate upwards periodically in order to graze in the productive upper layers. The carnivorous zooplankton could, of course, remain in the lower layer and prey on the migrating herbivores.

The coincidence of the layer of minimum concentration with the halocline suggests that the salinity change (1‰) in the halocline forms a barrier to the organisms. Yet, as pointed out above, some of the deeper organisms must move up through the halocline to feed. Taxonomic work and further sampling are necessary to determine the degree of exchange between the shallow zooplankton and the large population below the halocline.

The shallow and deep layers of maximum concentration persisted through night and day in all seasons, suggesting that they are permanent features of the vertical distribution of zooplankton in the Northeast Pacific.



FIG. 16. The variation of zooplankton in several depth intervals at station "P".

3. SEASONAL VARIATION

As shown in Fig. 17, a winter minimum, a summer maximum and a secondary autumn maximum marked the seasonal cycle of concentration in the surface zooplankton at station "P". Mean 24-hour surface concentration increased from about 20 g/1000 m³ during winter (December 1956 and January 1957) to a maximum of about 150 in the following summer, then fell to about 10 in early October 1957, before rising to about 30 g/1000 m³ to form the autumn maximum. Concentrations in December 1957 and January 1958 were slightly higher than in the previous year.

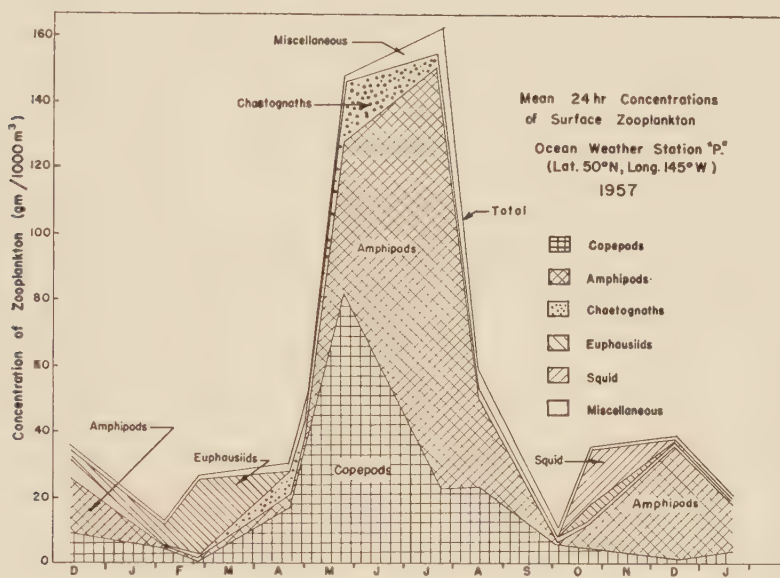


FIG. 17. Concentration and composition of surface zooplankton at station "P".

The concentration of zooplankton in the upper 150 m (Fig. 8) exhibited a seasonal cycle similar to the one at the surface. Concentrations averaged about 3.5 g/1000 m³ (range 0.3 to 5.0) during the winter of 1956-57 but were much higher, about 25 g/1000 m³ in the following early winter. The maximum concentrations were recorded in May and averaged about 80 g/1000 m³ (range 27 to 200). Although the highest concentrations were observed in May the trends (Fig. 8) suggest that the maximum was reached during June in an interval between two periods of observations. A small autumn maximum occurred in late October.

Vertical hauls from successive depths obtained between March 1957 and January 1958 are shown in Fig. 16. These data suggest that the seasonal cycle of abundance becomes much less marked below a depth of 200 m. The mean

concentrations for alternate 6-week periods within these dates exhibited a 10-fold variation in the upper 50 m, only 1- to 3-fold between depths of 200 and 500 m, and even less between 500 and 1000 m. Wiborg (1955) noted a similar phenomenon in the Norwegian Sea.

Ostvedt (1955) showed that the larger copepods at ocean weather station "M" in the Norwegian Sea descend from the upper layers in July and August to depths as great as 1000 to 2000 m and remain there until the onset of the next spring reproductive period in March and April when they again rise to the upper layers. Brodsky (1955) made similar observations in the Northwest Pacific Ocean.

While the data from station "P" are not sufficient to demonstrate this large-scale seasonal migration of copepods, they are consistent with Ostvedt's description. The larger species of copepods at station "P" were abundant in shallow hauls only during April and May, after which they occurred mainly in the deep hauls (300, 500 and 1000 m). Thus, it appears that in addition to growth, reproduction and mortality, vertical migration may be important in the seasonal variation of the abundance of copepods in the upper layers of the ocean.

Vertical and horizontal hauls gave contrasting pictures of the seasonal variation in gross taxonomic composition of the zooplankton. Typical vertical hauls at all times of year were composed of about 75% copepods, 15% chaetognaths and 10% miscellaneous groups. The contrasting seasonal variation of the taxonomic groups in the surface samples is shown in Fig. 17 (Table III). Amphipods were dominant in early winter in 1956, euphausiids in late winter, copepods in April and May, amphipods in mid-summer, squid and copepods in the fall, and amphipods again in the following winter.

TABLE III. Percentage composition of 24-hour mean catch of surface zooplankton at ocean weather station "P".

Date	Copepoda	Chaetognatha	Amphipoda	Euphausiacea	Squid	Others
	%	%	%	%	%	%
10-XII-56	27	15	49	9	...	...
7-II-57	34	3	1	62	...	...
27-II-57	1	tr.	5	92	...	2
25-IV-57	57	25	14	1	...	3
3-V-57	72	11	5	12	...	...
23-V-57	55	13	31	tr.	...	1
16-VII-57	14	3	80	...	...	3
13-VIII-57	4	1	87	tr.	5	3
4-X-57	54	6	3	3	26	8
18-X-57	13	2	21	13	51	...
20-XII-57	4	tr.	91	5	...	...
22-I-58	18	1	68	13	...	...
Mean	29.6	6.7	37.8	17.5	6.8	1.6

4. DIURNAL VARIATION

(a) SURFACE TOWS

A pronounced diurnal variation in the concentration of surface plankton was observed during each of the 24-hour series of bi-hourly surface tows taken at station "P" (Fig. 10, 11, 12, 13). The average of the ratios of mean night to mean day concentrations observed during 24-hour series of surface plankton hauls is about 8, with a range of 0.2 to 37.

Cushing (1951) in his excellent review of the diurnal vertical migrations of zooplankton, states that organisms undertaking a typical migration rise towards the surface during the evening, sink during the darkness near midnight, rise again before dawn and migrate actively downwards near sunrise. Thus, in the surface layer one would expect to find two nocturnal maxima of concentration separated by a minimum near midnight and low concentrations during the day.

Only 2 of the 12 surface series taken at station "P" conform exactly to Cushing's concept of a typical diurnal migration. Seven other series do exhibit two nocturnal maxima of concentration but also display one or more peaks of concentration during the daylight hours. Of the remaining 3 series, 1 reveals a daylight and a single nocturnal maximum, and two have a single maximum occurring at night (Fig. 10).

It is evident that the diurnal cycle of surface concentration was a variable one. However, the main features of the typical diurnal migration described by Cushing (1951) occurred in 9 of the 12 series, and mean night concentrations exceeded mean daylight concentrations in 10 series. The two instances in which day concentrations exceeded those observed at night occurred in the winter of 1957-58 and were associated with high daylight concentrations of amphipods (Fig. 13). Similar daylight maxima of amphipods were observed in December 1956. However, in the latter case a nocturnal increase in the concentration of copepods occurred and the mean night concentration exceeded the daylight average.

(b) VERTICAL HAULS

On six occasions vertical hauls from successive depths to the surface were made in the morning and after dark of the same day. The mean ratios of night/day concentrations for these hauls are presented in Table IV, and are greater than 1 in each case.

Wiborg (1955) compared night and day catches of zooplankton from surface tows and 25 and 100 m vertical hauls made at ocean weather station "M" in the Norwegian Sea. These ratios are also greater than 1 (Table IV).

The higher catches of zooplankton at night could result from diurnal vertical migration, or the ability of organisms to dodge nets in daylight.

TABLE IV. Mean ratios of night concentration to day concentration of zooplankton.

Depth of haul	Station "P"	Wiborg (1955)	King and Hida (1957)
		station "M"	Central Equatorial Pacific
<i>m</i>			
Surface	8.1	14.5	...
0 to 25	...	1.7	...
0 to 50	17.5(3.0)*	...	...
0 to 100	2.1	1.4	...
0 to 150	2.8	...	...
0 to 200	1.8	...	1.5
0 to 300	1.6	...	...
0 to 500	1.2	...	...

*The mean ratio for 0 to 50 m is lowered to 3.0 if one extremely high value is excluded.

On the average, the nocturnal increases in the percentage of the total zooplankton (0 to 500 m) to be found in some of the shallower depth intervals were accompanied by a decrease in the percentage present in the depth range from 300 to 500 m (Table V).

TABLE V. Diurnal variation of the proportion of the total zooplankton in the water column (0 to 500 m) present in various depth intervals at station "P". Figures shown are percentages of the total zooplankton taken in each day or night series.

Date	0-50 m		50-100 m		100-150 m		150-200 m		200-300 m		300-500 m	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
31-VII-57	76.1	24.2	0.3	5.3	0.3	2.1	23.0	34.2	0.3	33.8	...	...
15-VIII-57	4.7	13.2	6.5	0.0	19.6	2.6	0.0	4.4	0.0	18.9	69.0	61.0
8-X-57	13.6	30.8	0.0	0.0	23.2	6.2	1.1	53.7	6.5	9.3	55.5	0.0
28-X-57	1.3	14.6	8.6	0.0	11.8	0.0	0.0	1.0	23.8	56.3	54.4	28.1
23-XII-57	1.1	7.3	12.7	18.9	0.0	2.5	7.0	2.5	47.8	31.0	31.4	37.7
16-I-58	2.7	7.1	6.0	12.5	0.0	5.1	6.9	0.0	32.6	28.4	52.1	47.0
Mean*	4.7	14.5	6.8	6.3	10.9	3.3	3.0	12.3	22.1	28.6	52.5	35.0
Frequency with which Night percentage exceeded Day percentage												
	5/6		3/6		3/6		4/6		4/6		1/5	

*Percentages from 31-VII-57 excluded.

It would be attractive to assume that the nocturnal redistribution of zooplankton resulted from vertical migration. However, diurnal differences in the catches of zooplankton due to the ability of organisms to dodge nets in daylight must be greater in the shallow lighted layers than in the darker deep layers, since the diurnal range of light intensity decreases rapidly with depth (e.g., 0.5 to 0 langleys/min at the surface, 10⁻⁸ to 0 at about 300 m). The increased catches of zooplankton at night in the shallower layers would lead to an apparent decrease in the proportion of the total zooplankton to be found in the deeper layers.

The mean ratio of the *amount* of zooplankton present in the 300–500-meter layer at night to that in the daytime is only 1.1, while the average of the ratios in 5 depth intervals above 300 m is over 5 (see Fig. 18). The small nocturnal change below 300 m could be interpreted to support the theory that the apparent diurnal change in vertical distribution of the total zooplankton is due to a diurnal change in the vertical gradient of catchability. However, the low ratio of night/day amounts of plankton in the 300–500-meter layer could also result if the zooplankton migrating out of this layer at night was replaced by organisms moving up from even greater depths.

Wiborg commented on the difficulty of distinguishing between diurnal cycles of concentration, and diurnal variations in catchability, but nevertheless concluded from the decrease of the night/day ratio with depth that most diurnal vertical migration in the Norwegian Sea occurs within the upper 200 m of water.

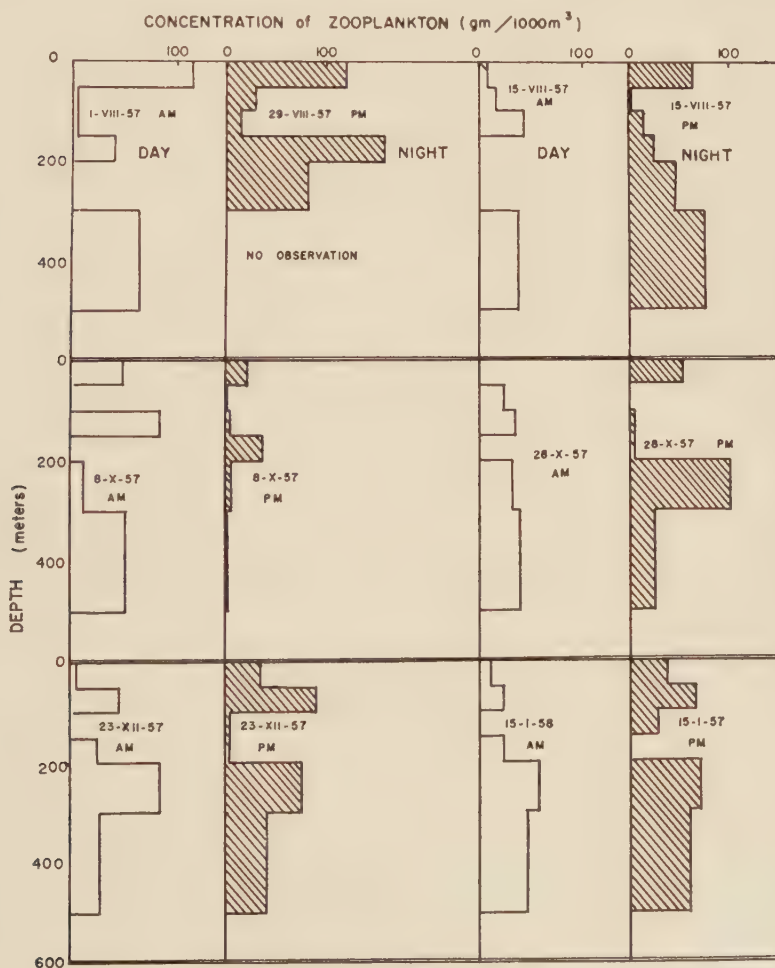


FIG. 18. Diurnal variation of zooplankton with depth at station "P".

King and Hida (1957) found that night catches were about $1\frac{1}{2}$ times the day catches from 200-meter oblique hauls in the central Equatorial Pacific (Table IV) and, like Wiborg, mentioned the difficulty of distinguishing between diurnal variation of concentration and variations in catchability. It will be seen that the night/day ratios found by Wiborg (1955) and King and Hida (1957) are within an order of magnitude of those observed at station "P". In view of their separation in distance, time, and technique, better agreement cannot be anticipated.

Although diurnal migration cannot be directly demonstrated from the present data it is certain that it occurs at least to some extent at station "P". Investigations by many authors (see Cushing, 1951) suggest its widespread occurrence and most of the 24-hour series of surface observations showed some of the major features of the typical migration described by Cushing.

5. SPECULATION ON THE AVAILABILITY OF ZOOPLANKTON AT STATION "P"

For the purposes of this discussion availability may be regarded as the fraction of the total zooplankton in a water column which a given fish could consume under the prevailing environmental conditions. The *amount* of zooplankton available would then be the product of the total zooplankton and the availability.

(a) AVAILABILITY AND DEPTH

The amount of zooplankton available to sight-feeding fish must partly depend on light as well as the concentration of zooplankton and other factors. The effect of the variation of light with depth on the availability will in turn depend on the vision of the fish in question.

Brett (1957) reports that juvenile coho salmon (*Oncorhynchus kisutch*) fed normally at light intensities between about 10^{-8} langley per minute (ly/min) and 0.2 ly/min, the highest light intensity used. Below 10^{-8} ly/min the rate of feeding decreased and at 10^{-9} ly/min it was only 3% of normal. Thus, reducing the light by a factor of 10 reduced the availability of food by a factor of about 30. In total darkness no feeding occurred. A light intensity of 10^{-8} ly/min may be regarded as the lower threshold illumination for normal feeding.

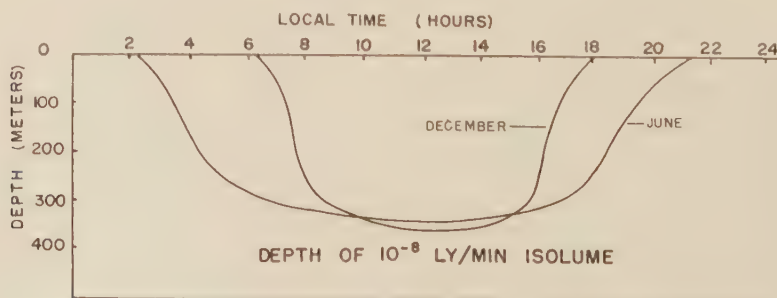


FIG. 19. Depths of the 10^{-8} langley/minute isolume at station "P".

The approximate depths of the 10^{-8} ly/min isolume at station "P" during a day in June and a day in December are presented in Fig. 19. It is evident that fish with vision similar to that of juvenile coho should be able to feed without light restriction down to maximum depths of 300–350 m. Thus, the layer of relatively rich zooplankton between 200 and 300 m would be readily available to such fish. However, factors such as salinity, temperature or pressure may prevent the fish from attaining this depth range. Also, if gradients in the zooplankton concentration affect the movements of feeding fish, the layer of minimum concentration between 100 and 200 m might deter them from moving down into the richer layer.

It is not known how representative the data on juvenile coho may be of the vision of other fish. Calculations from data on herring (Battle *et al.*, 1936; Marshall and Orr, 1955) suggest that the lower threshold illumination for normal feeding by these fish is somewhat greater than 10^{-7} ly/min. Grundfast (1932) reports that the lower limit of vision in *Lepomis* occurs at a light intensity equivalent to 10^{-11} ly/min. It has been pointed out (Strickland, 1958) that optimum feeding probably occurs at a higher light intensity.

Figure 19 suggests that the depth range through which fish may feed without light restriction is relatively constant through the daylight hours but becomes sharply reduced at night. Near sunset and sunrise unrestricted feeding may be limited to the top few meters. However, the results of surface sampling indicate that there is often a rich supply of food near the surface at these times.

(b) SEASONAL VARIATION

The seasonal cycle of zooplankton observed at station "P" doubtless reflects variations in the amount and kind of food available to sight feeding fish.

Seasonal variation in day length (e.g. Fig. 19) may tend to enhance the effect of the cycle of abundance on the zooplankton available to a given fish. During the summer zooplankton maximum the long days permit protracted feeding. In winter the coincidence of short days with generally sparse zooplankton suggests that the amounts available may be even less than are indicated by concentrations alone. It seems not impossible that winters with very sparse zooplankton, heavy cloud cover and unusual turbidity could be critical periods for the survival of young fish.

Seasonal variations in the response of zooplankton to light could also affect their availability. The tendency for amphipods at station "P" to occur at the surface usually near darkness in spring and mostly during broad daylight in early winter is a possible example.

(c) DIURNAL VARIATION

Diurnal ranges of composition and abundance in the surface zooplankton at station "P" may approach seasonal ranges but may or may not reflect diurnal cycles of availability.

If the diurnal variations result from vertical migration, the same organisms available to fish at the surface near dusk and dawn will occur at greater depths

during the daytime. If the diurnally migrating zooplankton maintain position within particular light intensities, as suggested by some workers (e.g. Kampa and Boden, 1954), their availability to fish may remain constant unless vertical variation of salinity, temperature and pressure restrict movement of the fish.

On the other hand, other workers (e.g. Clarke and Backus, 1956) suggest that on being stimulated to swim upward by a decrease in illumination, some organisms may rise into water having light intensities much higher than those originally inhabited. Presumably, the reverse would occur with decrease of light. In such cases, diurnal variations in availability are possible.

Marshall and Orr (1955) quote authors and mention evidence suggesting that young herring feed most actively from 5 to 9 p.m. and during a period near dawn, times when vertically migrating zooplankton should be near the surface (Cushing, 1951). Nemoto (1957) indicates that baleen whales tend to feed largely in the early morning and evening and suggests that this may be partly a response to the diurnal migrations of food organisms. Thus, it seems possible that plankton feeders as diverse as herring and whales may respond to diurnal cycles in the availability of food.

(d) GENERAL

Food supply must be one of the major factors affecting the occurrence, growth, movements and even survival of fish. General abundance of zooplankton has often been used as an index of feeding conditions and of the occurrence of fish. However, some studies suggest that general abundance alone is an incomplete criterion.

Thus, although Laevastu (1957) implies that catches of Pacific salmon (*Oncorhynchus* spp.) are greatest in regions of generally abundant zooplankton, Allen (1956a, b, c) noted discrepancies between the catches of vertical hauls and stomach contents of salmon. Vertical hauls caught mainly copepods while stomachs contained amphipods, squid and euphausiids, sometimes in pure culture and frequently as major fractions. Allen (1956c) suggests that surface samples would give a better indication of the occurrence of organisms known to be eaten by salmon than vertical hauls. The preliminary results from station "P" support Allen's suggestion.

Battle *et al.* (1936) found no relation between distributions of fatness of young Passamaquoddy herring and total zooplankton. Instead, fatness was found to be related to the distribution of surface zooplankton. This correlation must have resulted from the interaction of the vertical distribution of zooplankton and the feeding behaviour of the fish.

In addition to positive correlations between the occurrences of zooplankton and herring in the Barents Sea, Manteufel (1941) also found negative correlations, and at times none. As a result of detailed study, Manteufel was able to explain the varying relationship in terms of the life cycles and behaviour of both fish and zooplankton.

If knowledge of the effects of zooplankton on survival, growth, movements

and occurrence of fish is to pass the stage of crude qualitative correlation, many factors in addition to general abundance will require combined study. Light responses, depth ranges, behaviour, diurnal migration, diets of fish and rates of production of zooplankton are among these factors.

Separate study of many of these factors has been done, but only rarely have the results been combined in an attempt to understand food relationships. Use of a concept such as availability would be valuable in combining past results and in planning future zooplankton-fisheries work.

ACKNOWLEDGMENT

The writer wishes to thank Dr J. P. Tully and Dr J. D. H. Strickland for helpful criticism. R. J. LeBrasseur analysed the samples from the periods August–September 1956, November–December 1956, January–February 1957 and December–January 1957/58. The synoptic plankton data used here and the 150-meter vertical hauls made at station "P" form part of a program undertaken by the Marine Salmon Investigation at the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

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Contribution to the Biology of Herring (*Clupea harengus* L.) in Newfoundland Waters¹

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ABSTRACT

A study of the herring of the south and west coasts of Newfoundland in 1957 and 1958 revealed no great fluctuations in relative year-class strength and indicated a fairly high survival rate from the age of recruitment to the fishery.

The rate of growth was higher than that found by Tibbo (1956) in 1942-44, and no significant difference in growth rate was demonstrated between the south coast and the region of Bay of Islands and Port au Port Bay.

The study indicated an unusual spread in spawning time with probably peaks in spring, autumn and winter, while prior to about 1950 the Newfoundland herring were apparently all spring spawners. It is suggested that this has caused changes in the traditional pattern of distribution, which have been unfavourable for the herring fishery, and it may also have resulted in an actual decrease in population size.

INTRODUCTION

THE HERRING FISHERY in Newfoundland, which during and shortly after the war period was of a considerable magnitude, with a record of 164 million pounds landed in 1946, has over the last decade declined rapidly. This decline has been fairly uniform in all areas of the island, and to such an extent that only in the region of Bay of Islands and Port au Port Bay did a regular fishery of any significant proportion remain uninterrupted until last year.

Poor market conditions for herring products and other economic factors in the postwar period quite likely contributed to the decline of the herring fishery, but many people of the industry are of the opinion that the reduced landings have also been associated with a marked decrease in abundance of herring. Thus, in Fortune Bay, for instance, which previously was one of the centres of the herring fishery, no large quantities of herring have been observed for many years.

From 1942 to 1944 and again from 1946 to 1948, Tibbo (1956, 1957b) carried out herring investigations in Newfoundland waters, especially in the Fortune Bay and Bay of Islands areas. For the next 9 years some minor exploratory experiments were carried out in limited areas, but no general survey of the Newfoundland herring resources was conducted during this period.

Then, from June 1957 to September 1958 a project of herring research and exploratory fishing was undertaken by the Fisheries Research Board of Canada

¹Received for publication July 11, 1960.

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Biological Station, St. John's, Nfld., and with financial aid from the Industrial Development Service, Department of Fisheries of Canada.

The 57-foot M.V. *Matthew II*, chartered from the Newfoundland Department of Fisheries, was operated in exploratory fishing experiments with gill nets used as drift nets near the surface and as set nets at the bottom. The vessel was also used for searching with asdic/echo-sounder and for hydrographic and plankton surveys.

During summer and autumn both inshore and offshore waters on the south and west coasts were explored, but in the winter months operations were restricted to Placentia Bay and Fortune Bay on the south coast.

The results of the exploratory fishing and the echo surveys indicated that, during summer, the herring are sparsely distributed offshore in the warm surface layer of water, with possible aggregations off the west coast in areas of large horizontal temperature gradients. They may also, at this time of year, occasionally accumulate in the many bays and inlets of the island, but in the autumn, winter and spring they are found inshore more regularly and in larger concentrations.

The present paper is based on the material for biological statistics collected during the operation of the *Matthew II*, supplemented with a few samples obtained from local fishermen. Thus, it refers almost entirely to the herring on the south and west coasts of Newfoundland, as there is no material from the northeast coast, with the exception of 2 samples from White Bay and one from Trinity Bay.

MATERIAL AND METHODS

Table I gives a record of the samples, localities and methods of capture, and Fig. 1 shows the place names referred to in the table and elsewhere in this paper.

TABLE I. List of samples, localities and methods of capture.

Date	Locality	Total catch ^a	Sample			Method of capture	Size of nets, stretched mesh
			Scales	Lengths	Sex and maturity		
		numbers					inches
1957							
June 18	St. George's Bay	(5)	100	324	100	Drift nets	2 $\frac{7}{8}$
" 19	Bay of Islands	52	...	50	...	Set nets	2 $\frac{7}{8}$
" 23	Bonne Bay	55	...	54	...	Set nets	2 $\frac{7}{8}$
" 26	Hermitage Bay	...	86	86	86	Drift nets	unknown
" 27	Hermitage Bay	(2 $\frac{1}{2}$)	160	391	211	Drift nets	2 $\frac{7}{8}$
July 16	Hermitage Bay	18	...	18	18	Set nets	2 $\frac{7}{8}$
" 17	Hermitage Bay	188	186	186	186	Drift nets	2 $\frac{7}{8}$
" 18	Hermitage Bay	24	...	24	24	Set nets	2 $\frac{7}{8}$
" 19	Connaigre Bay	32	...	29	32	Drift nets	2 $\frac{7}{8}$
" 31	Off Bonne Bay	(11)	100	265	265	Drift nets	2 $\frac{7}{8}$

^aNumbers in brackets give quantity in barrels.

TABLE I—Continued

Aug.	1	Off Cow Head	58	...	58	58	Drift nets	$2\frac{7}{8}$
"	8	Off Point Riche	37	...	37	37	Drift nets	$2\frac{7}{8}$
"	9	Strait of Belle Isle	($1\frac{1}{2}$)	100	300	300	Drift nets	$2\frac{7}{8}$
"	9	Old Perlican, T.B.	...	65	65	65	Cod trap	unknown
"	17	Conche, White Bay	...	180	180	180	Set nets	unknown
"	28	Port aux Basques	45	...	44	44	Set nets	$2\frac{7}{8}$
"	29	Harbour Le Cou	...	100	162	162	Set nets	unknown
Sept.	23	Fortune Bay	60	54	54	54	Set nets	$2\frac{7}{8}$
"	25	Fortune Bay	30	...	18	17	Set nets	$2\frac{7}{8}$
"	26	Fortune Bay	20	19	19	19	Drift nets	$2\frac{7}{8}$
"	26	Fortune Bay	30	25	27	27	Set nets	$2\frac{7}{8}$
Oct.	16	Bay of Islands	1,185	237	957	957	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	17	Off Port au Port Bay	94	92	92	92	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	18	Off Port au Port Bay	646	130	644	514	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	19	Port au Port Bay	42	...	42	42	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$
"	19	Port au Port Bay	560	...	435	435	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	24	Bay of Islands	866	...	866	...	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	25	Bay of Islands	65	...	65	...	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
Nov.	8	Port au Port Bay	...	100	224	224	Purse seine	...
"	8	Port au Port Bay	...	...	165	...	Purse seine	...
"	19	Fortune Bay	51	...	51	51	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$

1958

Jan.	4	Fortune Bay	...	105	105	105	Set nets	unknown
"	21	Placentia Bay	($1\frac{1}{2}$)	116	416	116	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	24	Placentia Bay	47	47	47	47	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	29	Placentia Bay	79	...	79	79	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	29	Placentia Bay	320	100	320	100	Set nets	$2\frac{3}{4}$
"	29	Placentia Bay	316	...	316	...	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
Feb.	5	Fortune Bay	31	27	31	31	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	10	Fortune Bay	33	...	33	33	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
Mar.	14	Placentia Bay	355	100	337	100	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
April	1	Fortune Bay	15	...	12	12	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
May	4	Fortune Bay	...	...	45	45	Beach seine	unknown
"	5	Fortune Bay	...	...	612	162	Beach seine	unknown
June	3	Hermitage Bay	707	...	707	277	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$, $2\frac{7}{8}$
"	8	St. George's Bay	159	...	159	159	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$, $2\frac{7}{8}$
"	12	St. George's Bay	50	...	50	50	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$, $2\frac{7}{8}$
"	14	Hermitage Bay	225	...	223	223	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$, $2\frac{7}{8}$
"	18	St. Mary's Bay	388	...	388	388	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
July	9	Off Portland Hill	20	...	20	20	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$, $2\frac{7}{8}$
"	16	Bay of Islands	24	...	24	...	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	16	Bay of Islands	...	...	31	...	Set nets	unknown
"	17	Off Point Riche	67	...	67	67	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$, $2\frac{7}{8}$
"	21	Conche, White Bay	...	...	128	128	Set nets	unknown
"	26	Bonne Bay	41	...	41	41	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
"	31	Current Island	213	...	213	213	Set nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$
Aug.	27	Bay of Islands	39	...	39	...	Drift nets	$2\frac{1}{4}$, $2\frac{1}{2}$, $2\frac{3}{4}$, $2\frac{7}{8}$



FIG. 1. Location of place names referred to in the text.

Catches of less than approximately $\frac{1}{2}$ barrel were usually sampled in total. Most catches were very small and, in some cases, samples of several catches from the same area and caught during a short period of time have been combined.

The greatest total length was measured to the nearest $\frac{1}{2}$ centimetre (i.e. the distance from the tip of the lower jaw, with the mouth closed, to the end of the longest lobe of the caudal fin extended straight back in line with the body).

The gill nets are selective in their mode of fishing, and the length-frequency distributions were therefore adjusted for the effect of mesh selection by means of Holt's (1957) method, using the selection curves and the procedure described by the author in a previous paper (Olsen, 1959).

From the adjusted length-frequency distributions the age distributions were calculated by means of the age-length-key method.

The age determinations were made by means of the scales. It was observed that the first growth zone varied much in size and this is probably caused by the great spread in spawning time. However, the variation in size of the first growth zone appeared to be continuous, with no particular peaks. Therefore, no success was achieved in distinguishing between, for example, spring-spawned and autumn-spawned herring. The age was therefore determined as the number of completed growth zones and the first of January was arbitrarily chosen as the "birth date".

This procedure would lead to an underestimation of the age of fish spawned so late in the year that the first winter zone is not laid down in the scale (Jean, 1956) and the effect on the estimated age distribution would be to reduce the mean age and to dampen fluctuations in relative year-class strength, as discussed by Gulland (1955).

Condition of maturity was determined in 8 stages using the descriptions given by Aasen (1952). There was probably not complete consistency between the different field observers in determining the various degrees of ripening (stages III, IV, V and VIII), but they would have no difficulty in identifying a herring with running milt or roe, or a recently spent fish.

AGE AND GROWTH

AGE AND LENGTH DISTRIBUTION

In Fig. 2 and 3 are shown the age and length distributions adjusted for the effect of mesh selection for samples from various localities on the south and west coasts of Newfoundland.

In the summer samples from the west coast the length distributions do not differ very much; fairly large numbers of age-groups are represented in all samples and no particular year-class stands out as being exceptionally strong or weak.

The samples from the region of Bay of Islands and Port au Port Bay, taken in the autumn, differ considerably in age and length composition among themselves and on the whole they show some differences from the other west coast samples. The length curves are to some extent bimodal, the length range is usually greater

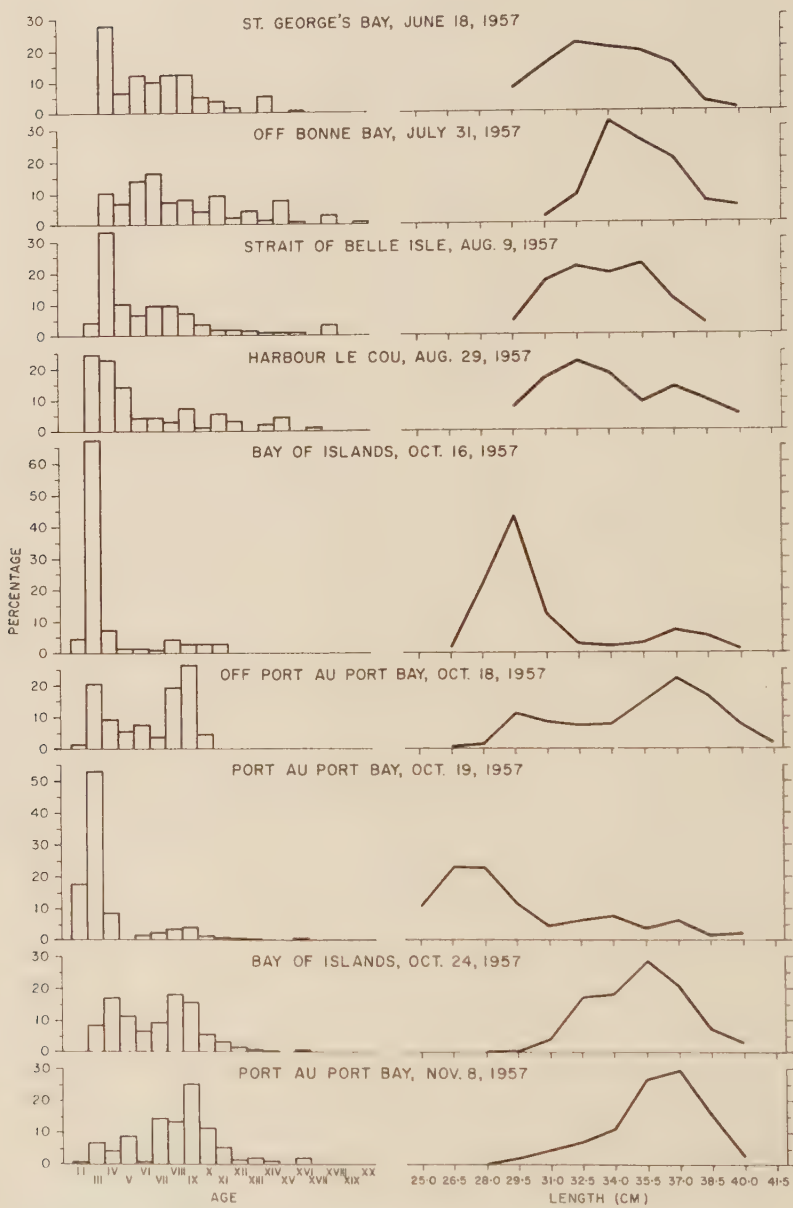


FIG. 2. Age and length distribution of herring samples in various localities from Harbour Le Cou to the Strait of Belle Isle.

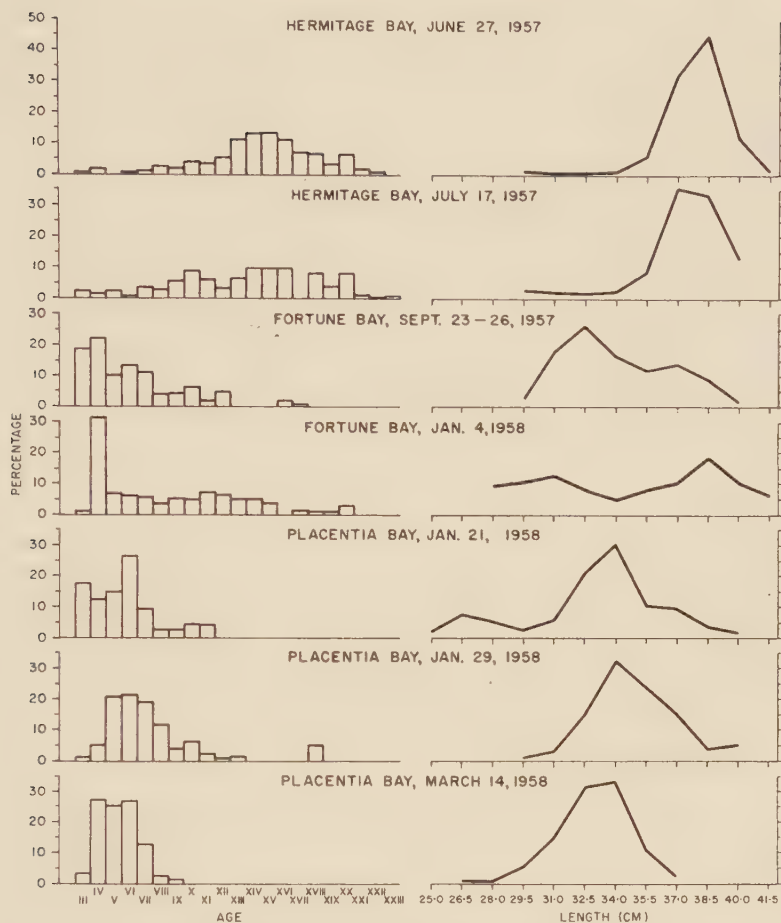


FIG. 3. Age and length distribution of herring samples from the south coast of Newfoundland.

and the age distributions are more irregular than those of the summer samples, and indicate fluctuations in year-class strength.

Thus, the VIII- and IX-groups were well represented in nearly all samples, and the VI-group was persistently weak. The greatest variation was found in the number of young fish below this age. Therefore, it would seem that in the same general area the catches were made up of herring 6 years or older mixed with varying amounts of younger fish. In some cases the young fish dominated, in others there were about equal amounts of both groups and in some catches the old fish were dominant.

On the south coast the herring in Hermitage Bay were very large and old, ranging from 3 to 23 years in age, with the peak at about age 14-15. The Fortune Bay herring were on an average smaller, but also in this bay a large number of age-groups were present, though with the younger fish in greatest abundance.

The smallest herring were found in Placentia Bay, which practically lacked fish over 12 years of age.

The herring fishery on the south coast has in the past decade been at a very low level, and unless the population size was extremely small, it is rather unlikely that the age composition has been much affected by the fishery.

Thus a trend of geographical segregation with age is indicated on the south coast, with a westward distribution of the large and old fish, and a concentration of the younger age-groups in the east, in Placentia Bay.

The data present no evidence of violent fluctuations in relative year-class strength, and in general the age distribution of the samples, particularly those from Hermitage Bay, would indicate a high survival rate after the age of recruitment to the fishery.

RATE OF GROWTH

In Fig. 4 the mean lengths are plotted against age at capture in 4 different areas, viz. Strait of Belle Isle, Bay of Islands and Port au Port Bay, Hermitage Bay, and Placentia Bay.

With the exception of the right-hand part of the Strait of Belle Isle curve, the mean length curves indicate a fairly uniform growth rate in all localities. The growth is rapid and quite appreciable right up to the high age of 20 years.

These observations differ from those of Tibbo (1956) in two ways. Firstly, the growth rate revealed by the present data is considerably higher than found by Tibbo in 1942-44 in any one area. The difference in mean lengths from

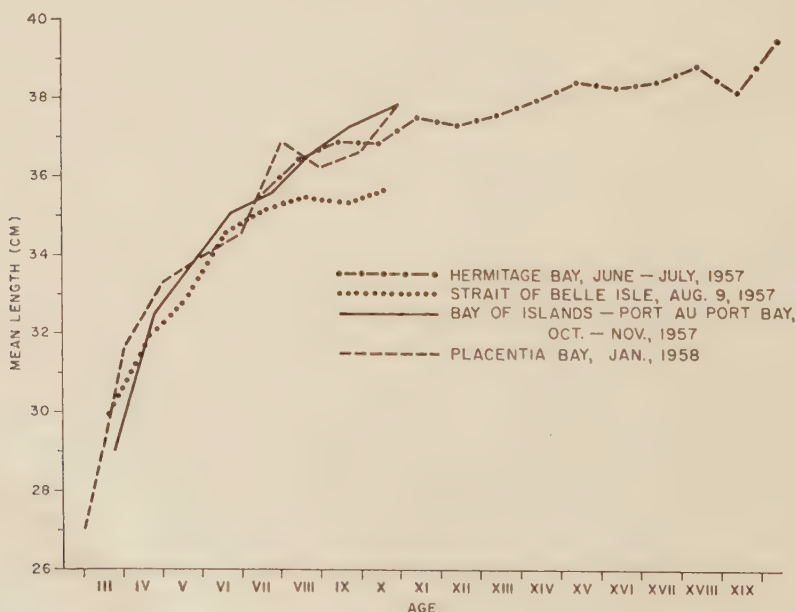


FIG. 4. Mean lengths plotted against age at capture in four different areas.

ages 5 to 10, for instance, between these and Tibbo's data from Fortune Bay increases with age from about 1 cm to over 2 cm.

Secondly, Tibbo demonstrated significant differences in growth rate between different areas, of which there is little evidence in the present data. In particular, the growth rate on the south coast seems to be very similar to that in the area of Bay of Islands to Port au Port Bay.

As pointed out by Tibbo, his growth curves are certain to be affected by gear selectivity, as no attempt was made to adjust for this effect. The effect would tend to reduce the calculated growth rate, as discussed by Ricker (1958, p. 187), and for comparison we should consider the magnitude of this reduction.

In Fig. 5, two mean length curves are shown for data from Bay of Islands and Port au Port Bay; one is adjusted for the effect of mesh selection, the other is unadjusted. Apparently the maximum difference in mean lengths, that at age 10+, is only of about 0.6 cm, and it is practically nil at the lower ages. Thus, it seems very unlikely that the effect of gear selection in Tibbo's estimates can account for anything but a small part of the difference in mean lengths between the present data and those of Tibbo.

The difficulties encountered in the interpretation of the first year's annulus in the scales, which have been mentioned before, might bias the age readings of the present material, but would not contribute to a larger error than one year

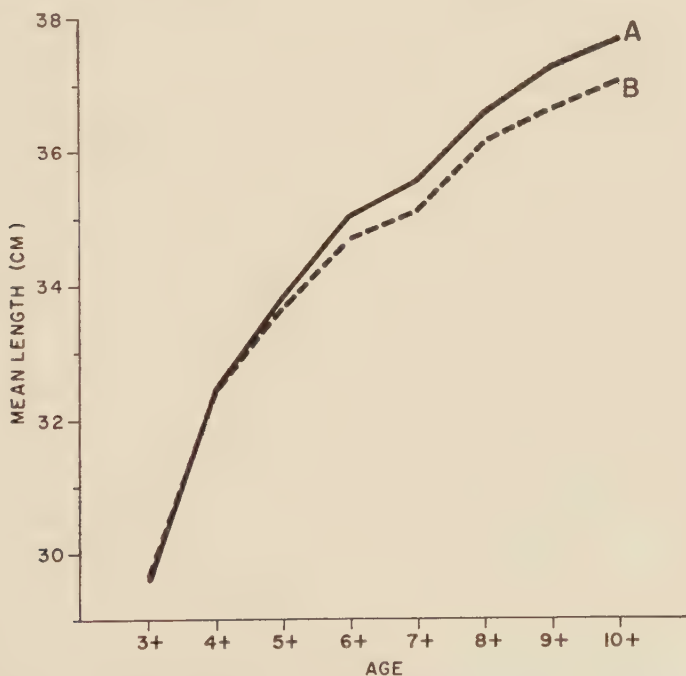


FIG. 5. Mean length curves for combined samples Bay of Islands-Port au Port Bay area. A—adjusted for effect of mesh selection. B—unadjusted.

in the individual fish, and on an average less. Even if we assume a consistent underreading of one full year, the mean lengths of the present data and those of Tibbo are considerably different. Consequently, unless there is something basically wrong in our age readings, the difference in growth rate is real.

In Tibbo's 1942-44 samples (Tibbo, 1956) from the south and west coasts of Newfoundland only a few herring of 37 cm or larger were present, and in his 1946-48 samples (Tibbo, 1957b) from the same areas few herring of 38 cm or larger were found.

This study indicates that herring of 37-39 cm are quite common in most localities, even excluding the very large fish in Hermitage Bay. This, of course, could be due to a greater survival in recent years, but would also be a result of a general increase in growth rate.

Thus, this investigation indicates that *the rate of growth of Newfoundland herring is at present considerably higher than in the years of the good fishery during the war and shortly afterwards*. Also, this study has revealed no significant difference in growth rates between the south coast and the area of Bay of Islands and Port au Port Bay.

REPRODUCTION

LENGTH AND AGE AT MATURITY

Most herring caught in Newfoundland are large, sexually mature fish, and the habitat of the immature (juvenile) part of the population is practically unknown.

During the present surveys only on a few occasions did the catches include appreciable amounts of immature herring, and from these it appeared that 50% of the herring of 27-28 cm had reached sexual maturity. The smallest mature fish was 24 cm and the largest immature one was 33.5 cm. This would indicate that the Newfoundland herring mature during the third to sixth year of life.

SPAWNING TIME

Table II records the percentages of herring in the various maturity stages from III to VIII in different localities and at different times; and Fig. 6 shows the percentage distribution by month for the entire material.

It appears that the numbers of herring in the spawning stage (VI), and, to some extent also the numbers of fish recently spent, are small, although samples were secured from all months of the year with the exception of April and December. Evidently this is partly a result of the nearly constant change in locality or area of fishing, but it is probably caused by the methods of fishing also. Whenever possible the method used was drift-netting near the surface and, consequently, no amount of spawning herring could be expected to be caught during these operations. Thus, the largest numbers of spawning herring were taken during the winter months when the nets were usually set at the bottom.

TABLE II. Percentage distribution of maturity stages. (Immature fish excluded.)

Date	Locality	Maturity stages in %						N
		III	IV	V	VI	VII	VIII	
1957								
June 18	St. George's Bay	...	3.0	1.0	...	96.0	...	100
June 26, 27	Hermitage Bay	8.1	41.0	28.1	...	20.0	2.7	295
July 16, 19	Hermitage Bay and Connaigre Bay	60.5	14.5	13.7	...	5.1	6.3	256
July 31, Aug. 1	Off Bonne Bay and Cow Head	38.0	45.6	6.4	...	2.1	7.9	329
Aug. 8, 9	Strait of Belle Isle and off Pt. Riche	45.1	36.2	12.5	...	...	4.2	335
Aug. 8, 9	Old Perlican, T.B.	18.8	56.3	21.9	...	...	3.1	64
Aug. 17	Conche	8.9	73.8	16.2	...	...	1.1	179
Aug. 28, 29	Port aux Basques and Hbr. Le Cou	15.6	64.8	18.1	...	...	1.5	199
Sept. 23-26	Fortune Bay	27.0	17.4	50.4	5.2	...	...	115
Oct. 16	Bay of Islands	85.1	12.3	1.7	0.4	...	0.6	701
Oct. 17, 18	Off Port au Port Bay	81.8	15.1	3.1	...	...	...	192
Oct. 19	Port au Port Bay	93.4	5.7	1.0	...	...	...	317
Nov. 8	Port au Port Bay	60.9	26.4	12.3	0.5	...	...	220
Nov. 19	Fortune Bay	94.5	2.8	...	...	...	2.8	36
1958								
Jan. 4	Fortune Bay	42.9	25.7	4.8	1.0	21.0	4.8	105
Jan. 21, 24	Placentia Bay	46.0	25.2	11.7	2.5	2.5	12.3	163
Jan. 29	Placentia Bay	13.4	6.1	11.2	12.3	19.6	36.9	179
Feb. 5-10	Fortune Bay	71.2	18.6	3.4	...	3.4	3.4	59
Mar. 14	Placentia Bay	28.0	25.0	14.0	2.0	...	31.0	100
May 4, 5	Fortune Bay	74.1	11.7	11.1	...	1.9	1.2	162
June 3	Hermitage Bay	64.4	6.8	0.5	...	3.2	25.2	222
June 18	St. Mary's Bay	47.8	17.1	1.6	1.0	...	32.6	387
July 9, 17	Off Portland Hill and Pt. Riche	64.4	27.6	4.6	...	1.2	2.3	87
July 21	Conche	62.7	13.5	1.6	...	...	22.2	126
July 26	Bonne Bay	79.0	...	...	10.5	10.5	...	19
July 31	Current Island	58.5	27.8	8.0	1.4	0.5	3.8	212

However, in spite of the lack of representative samples of herring in the actual spawning stage, some conclusions regarding the spawning time can be made from circumstantial evidence, such as the time distribution of nearly ripe (stage V) and recently spent (stage VII) fish.

The development of the gonads may be retarded for long periods when the herring inhabit cold waters, as mentioned by Tibbo (1956) and by Devold (1959). Consequently, the presence of nearly ripe fish does not necessarily infer that they are about to spawn shortly afterwards. On the other hand the recently spent herring recover rapidly, as stated by Tibbo (1957a) and by Aasen (1952).

Re-examining Table II we notice that the samples from the summer of 1957 included 2 groups which were distinctly out of phase as regards development of the gonads. In one group the gonads in the latter part of June showed evidence of a recent spawning, after which they recovered fairly quickly; and by the end of July to the beginning of August they had mostly reached maturity stage III. In June the other group already had fairly well developed gonads in stages IV and V. The ratio between the numbers in stages IV and V remained fairly steady

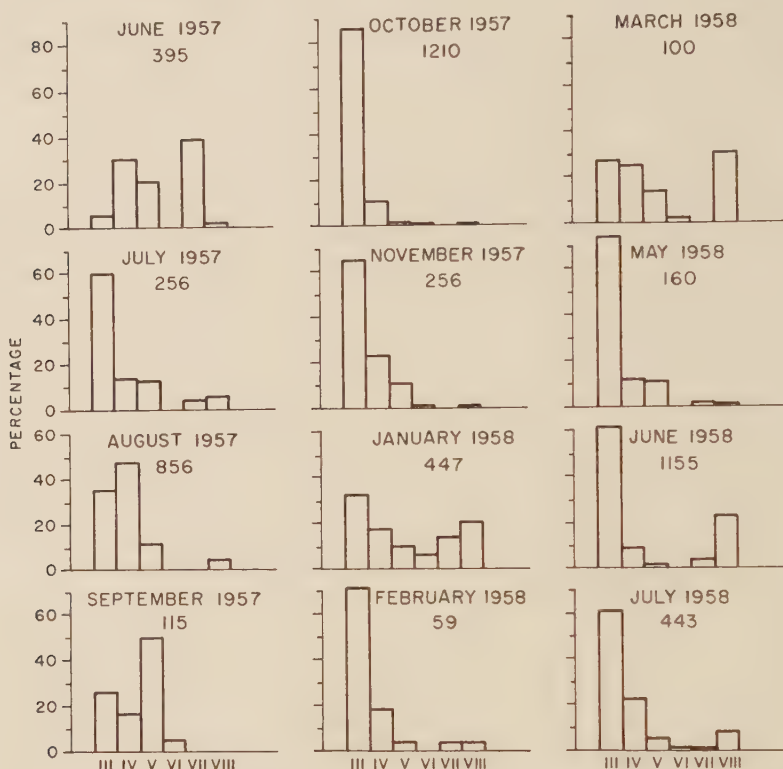


FIG. 6. Monthly percentage distribution of maturity stages III to VIII. All data combined.

during July and August, possibly because the herring become less vulnerable to drift-net fishing when they approach the spawning stage.

However, if we assume that these fish did not seek the very cold intermediate layer of water, and it is very unlikely that they would, their gonad development would progress fairly rapidly during the warm summer months, and they would most likely become ripe for spawning sometime in the autumn. Such a spawning is documented by the September samples from Fortune Bay, but in the later samples from 1957 there is only little evidence of this group of herring.

The winter samples from Placentia Bay and Fortune Bay clearly indicate a considerable spawning in December and January, although the catches also included many herring which probably would spawn later in the year.

The samples from the spring and summer of 1958 do not always conform with those from the previous year in the same localities, but the general picture of different spawning groups is confirmed.

The 3 samples from the northeast coast of Newfoundland do not indicate any appreciable difference from the general situation on the south and west coasts with regard to maturity distribution and thus to spawning time. Thus,

the present data give evidence of *an extreme spread in spawning time*, as was also indicated by the scale pattern. It is apparent that *some spawning herring may be found in Newfoundland waters in practically every month of the year*. The material does not suffice for an assessment of the relative importance of the seasons, but it would seem that *there is probably still a main spawning time in the spring*, in May and June, particularly on the west coast; *there is also some spawning in the autumn*; and, *at least on the south coast, a considerable winter spawning (December–January) takes place*.

• DISCUSSION

The age and growth analysis of this material did not reveal anything which gives a direct clue to the great decline in the herring fishery. However, the investigations have disclosed one feature of the biology of these herring which needs further consideration. This is the extreme spread in spawning time, which, as we have seen, is probably a fact in all Newfoundland waters, but particularly prevalent on the south coast.

One of the earliest published records with reference to the spawning time of the Newfoundland herring is probably contained in a report on the herring fishery of 1890 by the superintendent of fisheries, Mr Adolph Nielsen, who states (Newfoundland Fish. Comm. 1891, p. 29): "that Fortune Bay and Placentia Bay are the principal resorts of the herring, and that when they appear in these localities in the autumn and winter they can be classified as 'full herring', and in the spring they become 'spent herring'."

In subsequent reports during the next 25 to 30 years there are numerous references to the general spring spawning habit of the herring, such as this (Newfoundland Dept. Marine and Fisheries 1916, Appendix p. 26): "As usual these fish resorted to their old haunts, in the shoal waters and muddy bottoms of the arms and bays at the usual time—the latter part of May and early June—in increased numbers for the purpose of spawning." This is also confirmed by Hjort (1915, p. 10) who briefly states: "The herring from the west coast of Newfoundland are spring spawners"; and Thompson (1931, p. 36) generally refers to the herring as spring spawners.

However, from some of the old reports it would appear that the spawning time was not always restricted to the spring months, but might in some years have included the month of July as well (Newfoundland Fish. Comm. 1892, p. 81; and Newfoundland Dept. Marine and Fisheries, 1907, Appendix p. 41).

From the investigations carried out by Tibbo (1956, p. 461) it appears that the spawning time in 1943 was from June 5 to 20 on the east coast, from May 24 to June 20 on the west coast, and from May 12 to June 5 on the south coast. Similarly, on the basis of his 1946–48 material, Tibbo (1957b, p. 160) concluded: "that spawning in some seasons, at least, is not completed until after the middle of June."

It would therefore appear that *all reports of observations prior to 1949 indicate that the Newfoundland herring were spring spawners*. The spawning may sometimes have been extended into the early part of the summer, but there is complete lack of evidence of any major departure from the "normal" spring spawning.

The first evidence of a change in spawning time was reported by Squires (1957), who in late September 1955 found pelagic herring larvae in the northern part of the Gulf of St. Lawrence. Mr Squires has kindly informed me that these larvae ranged from 5.2 to 19.1 mm in length, and in particular those caught near the Newfoundland coast (Sta. No. 10, 18 and 21) were quite small, not exceeding 12.0 mm. According to Bigelow and Schroeder (1953, p. 91) the herring is about 5-6 mm long at hatching. Thus, there can be no doubt that these herring larvae were derived from nearby spawning grounds, and at least some of them were spawned in Newfoundland waters.

A further observation of a departure in recent years from the usual spring spawning is reported by Tibbo (1959, p. 30), who, from summer experiments with drift nets at the south coast of Newfoundland in 1956 and 1957 concluded that: "the spawning season extended over a considerable portion of the summer."

The present study fully confirms these observations, and as we have seen, it also indicates a spawning in the winter as well as in the spring and autumn.

It seems quite improbable that the presence of significant numbers of herring spawning in the autumn and winter would have escaped notice at the time that systematic and detailed investigations of the Newfoundland herring were conducted by Tibbo. Consequently, we are led to conclude that *some time during the last 10-12 years (perhaps gradually) the Newfoundland herring, which for at least the previous 60 years had been spawning in the spring or early summer, changed their spawning habit so that now some spawning seems to occur in practically every month of the year*. This period coincides with the time of a grave decline in the herring fishery, but this in itself is not very surprising, because a change of this nature would affect the fishery in several ways.

Firstly, any change in spawning habits must be associated with changes in the usual migratory pattern and general distribution of the herring. In particular, because of the seasonal warming of the surface layer of water, a change from spring spawning to spawning later in the season would tend to move the herring into deeper waters and farther offshore when they come in to spawn.

The Newfoundland herring fishery is basically a shore fishery on spawning or pre-spawning concentrations. With the exception of a small purse-seine fishery on the west coast, the gears and vessels used are rather primitive and thus are not very versatile or adaptable to changes in the "normal" distribution and behaviour of the herring and are probably quite incapable of coping with a shift towards deeper waters farther offshore.

There is another aspect which may have been of even greater impact: the herring is a migratory species which changes habitat regularly with the season. Thus, the spawning grounds are usually different from the main feeding areas. In most herring populations there is a well defined and relatively short spawning

spawn and the whole bulk of the adult population recovers from spawning and undergoes every other phase of physiological development at about the same time of the year. Therefore, they tend to occur in concentrated bodies and undertake mass migrations to the various habitats as the seasons change.

Apparently in Newfoundland waters at present some herring are spawning while another group is in the main feeding stage and, as we have seen, all intermediate stages of development can be found at the same time, although with peaks at some particular times of the year.

The effect of this situation might be a general dispersion of the herring. Thus, on the south coast, where probably the spread in spawning time is most extreme, no large concentrations of herring comparable to those experienced prior to 1943, say, have been observed for many years and the traditional Fortune Bay fishery has ceased to exist. On the other hand, the herring accumulating in the Bay of Islands-Port au Port Bay area in late autumn appeared still to be mainly spring spawners and it is noted that the purse seine fishery in this area remained uninterrupted until 1959.

Finally, one may raise the question of what effect such an unusual spread in spawning time as the study indicates may have on the recruitment, and thereby on the absolute size of the population. The fishermen complain about the herring being less abundant than previously, but this could merely be an effect of a change in availability and, in fact, no data exist on which any sound assessment of present, past or future population size can be founded. We can, therefore, only theorize about what effect a great spread in spawning time might have on the population size.

Some of the larger herring populations, and in particular those of great abundance, are characterized by one relatively short and well defined spawning period. Despite in very rare cases two, one would be tempted to believe that this condition, as a result of "the survival of the fittest", is the one which provides the best recruitment and thus safeguards the survival of the species. If this be true it can be expected that the change towards the great spread in spawning time has not only affected the availability of the Newfoundland herring but has also caused a reduction of the population size. This would explain the decreased growth rate mentioned previously, if we assume that the rate of growth is density dependent.

Considerable changes in spawning time are also known in other herring populations, and the idea that such changes have marked effects on the fishery is by no means new.

Thus, Devold (1959) suggests that the periodic disappearance of the Atlanto-Scandinavian herring from their usual spawning grounds off the Norwegian west coast is associated with an advancement of the spawning time of several months. The herring will then approach the Norwegian west coast too early to find suitable hydrographic conditions for spawning and proceed into Skagerrak to spawn at the Norwegian Skagerak coast and the Swedish west coast.

The case of the Newfoundland herring is not a direct parallel, but it has

general interest and should be watched further. Because of the present extremity with regard to spawning conditions in this population, it might provide a rare opportunity to study how a fish population is affected by factors of this nature.

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A Method for Preparing Glycerin-Stored Otoliths for Age Determination¹

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ABSTRACT

Glycerin-preserved otoliths of burbot, *Lota lota*, often become opaque and difficult to age; they become readable if heated in glycerin for 10 minutes at 190°C, or for longer times at lower temperatures.

INTRODUCTION

SCALES, OTOLITHS, AND BONES or bony structures are frequently used for determining the age of freshwater fish. The burbot, *Lota lota*, has scales which are small, embedded, and scarcely noticeable, so the otoliths are used in age determinations. Under field conditions, it is often impractical to determine ages from fresh material and thus the otoliths must be held in a storage medium for an indefinite period. Otoliths from Heming Lake burbot were held in 50% glycerin in water and were found to be too opaque to allow adequate transmission of light even after grinding, and the annual growth rings were not clearly visible. Rather than discard the otoliths, an attempt was made to prepare them so that annual rings might become clear enough to permit age determination. Heating the otoliths caused browning which tended to accentuate the dark and light areas of growth and made age determination easier. The technique is presented here.

MATERIALS AND METHODS

Opaque otoliths preserved 4 months in 50% glycerin in water were washed in water and then wiped dry. The otoliths were first ground on a fine carborundum stone to facilitate light transmission. Reflected light was not used for examining otoliths in this experiment. They were then placed in porcelain crucibles. Some otoliths were covered with a drop of pure glycerin, others were not treated with glycerin, in order to see if the two methods differed.

The crucibles containing otoliths were heated in a drying oven at various temperatures ranging from 140°C to 200°C and were removed from the oven at time intervals from 5 minutes to 1 hour. A few samples were treated at temperatures above and below this range.

¹Received for publication July 4, 1960.

RESULTS

The basic technique was discovered accidentally. Storage in glycerin was presumed to cause the opacity which often develops so it seemed logical that if the glycerin was driven off the annual rings might become more plainly visible. To expedite drying, the otoliths were heated in an oven rather than air-dried. No particular attention was given to the time of drying nor to the temperature; however, when the otolith was examined under a binocular microscope the annual rings were slightly more pronounced than they had been prior to drying. The improvement was at first attributed to the drying process which had browned the otolith through charring. Further experience suggested that perhaps the charring *per se* was not responsible for the differentiation of dark and light areas, but rather that the glycerin had not penetrated the otolith uniformly and had caused differential staining. Therefore a few otoliths were tested by placing them in a crucible containing glycerin and allowing them to cook in this medium. It was found that the otoliths browned much faster in glycerin and that the annual rings were much more pronounced (Fig. 1). The glycerin itself browned on

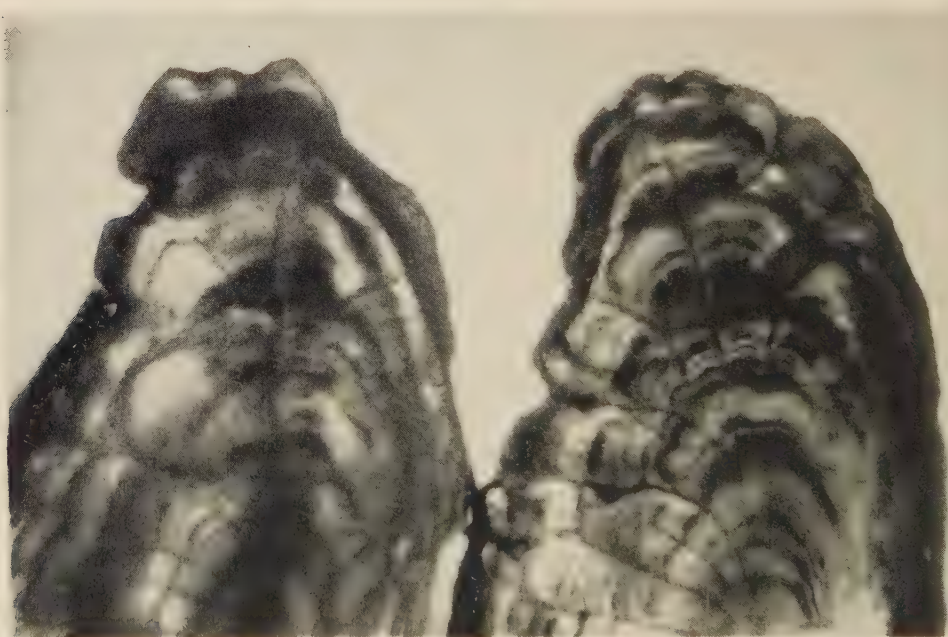


FIG. 1. Photomicrograph ($\times 10$) of a pair of otoliths by transmitted light. The effect of heating in glycerin is shown by the increased definition of the opaque areas on the right.

heating. As this treatment held promise of improving the quality of otoliths for age determinations, the method was tested under controlled temperature conditions. The results of the tests without and with glycerin are shown in Tables I and II, respectively.

Table I shows that otoliths stored in glycerin but washed and then heated without the addition of glycerin did become differentially browned. Relatively high temperatures for prolonged periods of time were required before the annual rings were readily noticeable. Too-high temperatures charred the otolith and

TABLE I. Time-temperature relationship for effects of heating burbot otoliths in an oven, without addition of glycerin. 0-No change; X-Slight browning but annual rings not clear; *-Brown in colour and annual rings outstanding; •-So dark that the annual ring was obscured.

Temp. °C	Time in minutes									
	5	10	15	20	25	30	35	40	45	
110	0	0	0	0	0	0	0	0	0	
125	0	0	0	0	0	0	0	0	0	
140	0	0	0	0	0	0	0	0	0	
155	0	0	0	0	0	0	0	0	0	
170	0	0	0	0	0	0	X	X	X	
185	0	0	X	X	X	X	X	X	*	
200	0	0	X	X	X	X	X	*	*	
225	0	X	•	•	•	•	•	•	•	

rendered it useless. Temperatures between 110°C and 155°C did not improve the readability of the otoliths and were classed as having had no effect. At 170°C some browning effect was noted after 35 minutes, but the annual rings were still not very evident. At 185°, after 45 minutes the annual rings were very clear. After 40 minutes at 200°C the annual rings were much more pronounced than at the previous temperatures. At 225°C the otoliths were so charred after 15 minutes that they were useless for age determinations.

From Table II it is clearly evident that the addition of glycerin before heating improved the technique. The otoliths browned more easily at lower

TABLE II. Time-temperature relationship for effects of heating burbot otoliths in an oven, with glycerin added to the crucible. Symbols as in Table I.

Temp. °C	Time in minutes									
	5	10	15	20	25	30	35	40	45	
155	0	0	0	X	X	X	X	X	X	
160	0	0	X	X	X	X	X	X	X	
165	0	0	X	X	*	*	*	*	*	
170	0	0	X	X	*	*	*	*	*	
175	0	0	X	*	*	*	*	*	*	
180	0	X	X	*	*	*	*	*	*	
185	X	*	*	*	*	*	*	*	*	
190	X	*	*	*	*	*	*	*	*	
195	X	*	*	*	*	*	*	*	●	

temperatures. At 155°C some browning was noted after 15 minutes but continued exposure at this temperature did not differentiate the growth areas even after 45 minutes. A rise of 5°C to 160°C made little difference in the appearance of the otolith. At a temperature of 165°C however, the annual rings were clearly visible after 25 minutes exposure. Further increases in temperature resulted in a reduction in the time required to produce the desired effect, for example, over the temperature range 185° to 195°C the annual rings stood out after only 10 minutes in the oven.

DISCUSSION

Burbot otoliths stored in glycerin may become opaque, resulting in the disappearance of the annual rings. Heating as described above either chars the otolith differentially or causes the glycerin to brown, the effect of which is noticed more in the translucent rings.

Whether it is the effect of heating *per se* or the addition of glycerin in combination with the heat that produces the end results is still in doubt. However, this method has proved of considerable use, for the junior author has treated (with remarkable effectiveness) otoliths removed in 1959 and stored for at least 4 months. This technique did not require a great deal of preparation, and the final results justified the time required as it was possible to assign ages to otoliths that were unreadable. Other species of fish, in which the otoliths are large and thick, may react differently. The burbot otoliths used in this experiment were not thick, having been taken from fish the largest of which was 21 inches (53 cm) in length.

Phytoplankton of the *Calanus* Expeditions in Hudson Bay, 1953 and 1954¹

"CALANUS" SERIES, No. 18

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ABSTRACT

Phytoplankton samples, collected in 1953 and 1954 by the *Calanus* expeditions, were examined by the quantitative sedimentation method in an attempt to determine the ecological aspects of phytoplankton production in Hudson Bay and Strait. During the period July to September of both years, water temperature data, and salinity, oxygen and quantitative phytoplankton samples were collected at the surface and from depths of 10, 25, 50 and 100 metres. Numerically, the most abundant, heterogeneous phytoplankton populations were found in the mouth of Hudson Bay. The lower production of phytoplankton in the surface layer can be explained by the greater amplitude of temperature and salinity, dependent upon ice conditions and surface wind drift. The most productive layer was at a depth of 10 m. Large phytoplankton populations in waters supersaturated with oxygen were still found at 25 m, indicating light conditions favourable for photosynthesis. The relatively high plankton production in the area joining Hudson Bay and Hudson Strait is probably due to the hydrographic structure and the supply of nutrients resulting from the mixing of water masses which originate in other geographical areas. The preponderance of diatoms over flagellated groups, which is more marked in Hudson Strait than in Hudson Bay,

Received for publication July 15, 1958; as revised, October 25, 1960.

is typical for the arctic. The composition of phytoplankton in these areas shows a great similarity in the main to that found on both sides of the Atlantic. Apart from locally produced plankton populations, there is a population exchange which follows water movements. To supplement the meagreness of existing taxonomic descriptions, attention is here focussed on the identification of plankters and their individual importance in the general ecology of the phytoplankton.

INTRODUCTION

DURING THE SUMMERS OF 1953 AND 1954, the M.V. *Calanus* investigations of the Fisheries Research Board of Canada were carried out in northern Hudson Bay and western Hudson Strait. Part of the scientific programme consisted of phytoplankton sampling, the results of which are reported here.

Sampling was done during the periods July 21 to 30, August 3 to 17 and September 2 to 16 in 1953, and July 22 to 24, August 3 to 21 and September 4 to 16 in 1954. Station locations, shown in Fig. 1, are described by Grainger and Dunbar (1956).

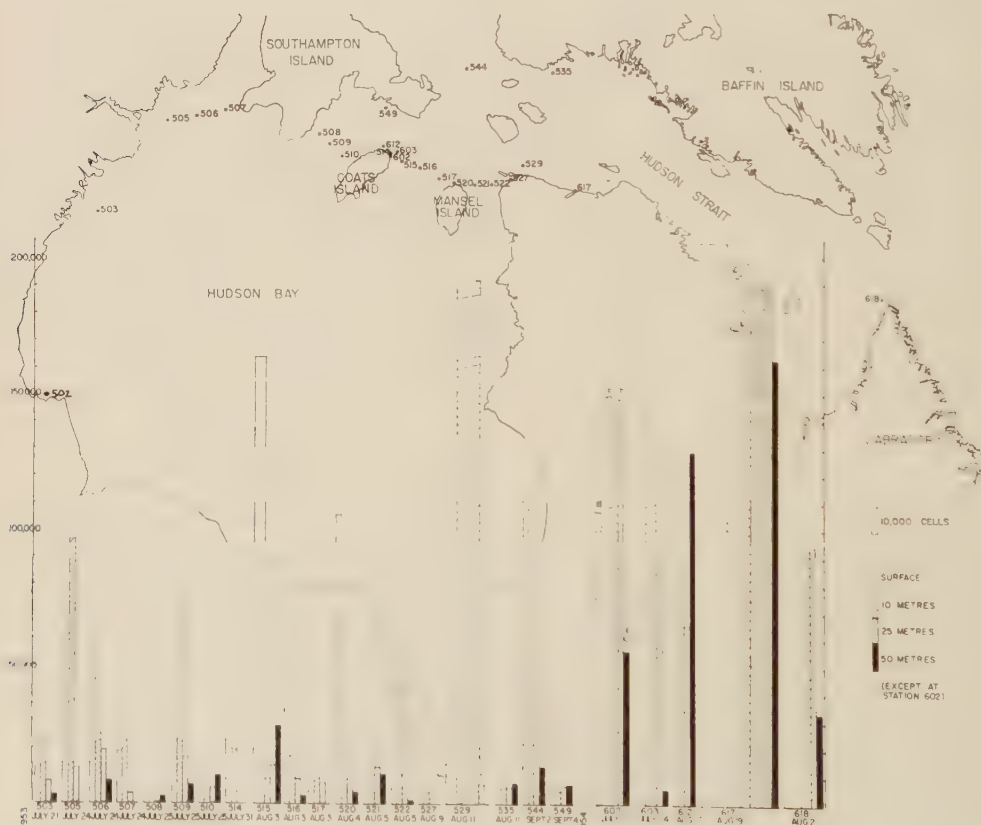


FIG. 1. Histogram-map showing vertical and horizontal distribution of diatoms and dinoflagellates in Hudson Bay and Hudson Strait. Numbers on the left scale refer to single columns. Lines at the top of the histogram bars show the number of columns per bar.

Seven areas, where quantitative and qualitative plankton stations were occupied, have been distinguished in northern Hudson Bay and Hudson Strait.

1. The western Hudson Bay coastal area, including stations 502, 503, 551, 553 and 555.
2. The area between Chesterfield Inlet and Southampton Island (Cape Kendall), including stations 505, 506 and 507.
3. The northern parts of Hudson Bay, including stations 508, 509, 510, 512, 549 and 612, located in Fisher and Evans Straits and south Foxe Channel.
4. The area between Coats and Mansel Islands, including stations 515, 516, 517 and 520.
5. The area between Cape Wolstenholme (northwest Quebec) and Mansel Island, including stations 521, 522, 527 and 529.
6. The west Hudson Strait area, including stations 531 and 535, and the Sugluk and Nuvuk stations 526 and 617.
7. The east end of Hudson Strait, including station 618.

PREVIOUS INVESTIGATIONS

The history of phytoplankton investigations in the Canadian eastern arctic is brief. The only previous work in Hudson Bay was done by Davidson (1931) who made quantitative and qualitative studies on phytoplankton collected with fine silk nets by the trawler *Loubyrne* in August and September of 1930. A series of collections was made by Polunin (1934) in Ungava Bay, at Akpatok Island.

The eastern arctic waters have been investigated by various foreign expeditions. The Nares expedition (1875–76) to Ellesmere Island and north Greenland collected the first dinoflagellates, reported by Dickie (1878), and diatoms, described by Cleve (1883). The ship *Michael Sars* in 1924, with Gran on board, collected plankton from five stations in Davis Strait (Seidenfaden, 1947). Much information on the ecology and taxonomy of arctic phytoplankton, including thecate dinoflagellates, was assembled by the Godthaab Expedition (Grøntved and Seidenfaden, 1938).

These are the more important contributions to our knowledge of the phytoplankton in eastern Canadian arctic waters. The collective papers of Whelden (1947) on algae, Seidenfaden (1947) on marine phytoplankton, Ross (1947) on freshwater diatoms and Holmes (1956) on central Labrador Sea collections, complete the list of literature. The Labrador Sea phytoplankton was found to be neither strictly arctic, boreal nor temperate, and neither completely oceanic nor neritic. Since this vast area is still largely unexplored for phytoplankton, our knowledge of the composition, distribution and production of plankton remains scant. It is not only of pure theoretical scientific interest but also a practical necessity to understand the general biological economy of the arctic.

METHODS

Water samples, collected in Nansen reversing water bottles, and preserved in 5% neutral formalin, were used for quantitative phytoplankton studies. They were stored in approximately 170-ml glass bottles with bakelite screw caps. Before sedimentation of the samples, each sample was shaken 20 times to ensure even mixing of plankton. It was found that too energetic shaking of the bottle containing plankton breaks the longer chains of *Thalassiosira* and *Chaetoceros* into small fragments, making counting and identification tedious. The Utermöhl inverted microscope was used for quantitative estimations, with the prismatic ocular $\times 8$ being used for counting. Objectives of 10, 25 and 40 powers were used according to the frequency of species and their size. The larger, less numerous forms were examined, with objective $\times 10$, in a 25-ml cylinder; smaller, more numerous forms, with objectives $\times 25$ or $\times 40$, in 10- or 5-ml cylinders. Samples containing a moderate number of species and small populations of so-called gamma or μ -plankton were examined in 25-ml cylinders. In a few instances the original water was diluted with distilled water 1 to 1, then examined. Rare species and those difficult to identify were isolated from the cylinders with a pipette, then observed under the high power of a compound microscope. Quantitative samples were usually examined after 15 or 20 hours of settling. Plankton nets of numbers 20 and 5 silk mesh, hauled horizontally and vertically, were used for qualitative studies. Diatoms of net hauls were washed in distilled water, boiled with acid, then washed again, for making temporary preparations. All drawings were made with *camera lucida*. Front phase illumination was also used for taxonomic identification of dinoflagellates and other forms. All cells in chains were individually counted.

HYDROGRAPHIC CONDITIONS

Hydrographic conditions in northern Hudson Bay and western Hudson Strait have been described most recently by Dunbar (1958) and Campbell (1959), the former using *Calanus* material collected from stations discussed here. While the most northwesterly stations show the influence of arctic water flowing southward into Hudson Bay through Roes Welcome Sound, those of northeast Hudson Bay and west Hudson Strait are in a region showing complex hydrographic conditions, where arctic waters from Foxe Channel and warmer waters from southern Hudson Bay converge. Present data from the area under consideration do not permit a real assessment of the relation of the phytoplankton to temperature, since no continuous records are available from any one location. It appears however that phytoplankton populations are greater in those areas where various water masses mix.

Ice is a factor of extreme importance, and a highly variable one from year to year. The holophytic plant societies especially are affected by ice cover influencing light, salinity and temperature conditions, and diatom spring maxima may be delayed for many weeks by a persistent ice cover (Braarud and Hope,

1952). Open leads in the ice cover are probably of considerable importance in allowing sufficient illumination for photosynthesis in very local areas.

The physiological effect of changing salinities in the sea cannot be separated from the influence of temperature acting simultaneously. Various dinoflagellates have their own optima of growth and development as far as salinities are concerned (Braarud, 1951). Surface waters of the studied area, covered with melting ice in summer and autumn, are especially exposed to rapid temperature and salinity changes. Such conditions do not favour metabolic activities of plankton, producing osmotic barriers for the typical euryhaline species. Lower salinities close to the under surface of the ice are found when ice melts; when it is solid salinities are higher, and allow rich growth of the diatom film. Observations of the author during the H.M.C.S. *Labrador* cruise in 1956 show that green-brown films of diatoms occurred under the ice turned up by the ice-breaker around Baffin Island. Special observations carried out on the naked genera of dinoflagellates show that some genera, for example *Gymnodinium*, *Gyrodinium*, *Amphidinium* and *Massartia*, are rare in the vicinity of ice while they occur more frequently in the leads. Some typical marine species show definite resistance to varying salinities in the coastal area. *Goniaulax tamarensis*, according to the author's observations, is specially adapted to changing salinities by immediate production of thin-membraned cysts. *Ceratium* species, when swept into brackish lagoons, become strongly plasmolized or reject their flagella, or the whole protoplasm escapes from the cell-membrane, as observed by the present writer in the Point Barrow area of Alaska. It is possible that freshwater *Dinobryon* species have great adaptability to marine conditions since large populations of this chrysomonad, with cysts, were found by the author in the sea in good condition. *Scenedesmus*, *Oocystis* and *Ankistrodesmus*, swept from ice pools, perish after a few days in the sea.

The oxygen data collected indicate well-oxygenated surface and even deeper layers, where phytoplankton was found in sufficient quantities to cause it. The surface-to-25-metre layer shows supersaturation of oxygen at stations 502, 503, 505, 508, 510, 520 and 527. It is to a certain degree in agreement with Nutt and Coachman's (1956) observations on oxygen distribution in Hebron Fjord, Labrador. Subsaturated surface water occurred in 1953 at stations 517 and 544, in 1954 at stations 502, 612 and 617. This is not understood since large diatom populations were found at these stations. At 25 metres only five subsaturated samples were recorded. At 50 m there was slight supersaturation at nine stations.

DETRITUS

Special emphasis has been given to leptonel in the sea, to its importance in biological cycles involving the release of organic nitrogen and phosphorus by bacteria and the reassimilation of these soluble molecules by phytoplankton, and to the amounts of leptonel and populations of living communities (Goldberg, Baker and Fox, 1952; Fox, Isaacs and Corcoran, 1952). Identification of water

masses by their suspended particles was carried out by Atkins and Jenkins (1955), Burt (1955) and Gran and Braarud (1935), who found large concentrations of detritus in quantitative samples from the Gulf of Maine, where it affects the phytoplankton production.

In the present collection detritus occurred in many stations in sedimentation cylinders in the form of amorphous organic particles or as long fibres derived from various plant tissues. The largest concentrations of detritus were observed in the neritic stations 527, 535, 529, 506, 507, 508, 612 and 618, which were located in shallow water. At some detritus was distributed evenly from the surface to the bottom, while at station 509 little detritus was found at the surface, but a dense concentration occurred at 10 metres depth. At station 508 large concentrations were found at 25 m and 80 m, while the top samples contained only small quantities of detritus.

Phytoplankton samples containing large concentrations of detritus had poor populations and reduced numbers of species in contrast with samples with no detritus.

The main detritus supply in the arctic comes from the sea floor deposits, rivers and lakes, and is swept from the land by wind and rain into the sea. Huge quantities of detritus are found in the arctic ice. During melting of the sea ice, arctic waters show reduced transparency because of the ice-detritus. Turbulent or stormy waters contain both mineral and organic detritus. The heavier mineral particles after a few days sink and remain at the bottom, while lighter organic detritus may remain longer in suspension. The particles of detritus serve as attachment surfaces for bacteria, which affect the physiological metabolism of the phytoplankton. According to Burkholder and Burkholder (1956), suspended particles are important in the vitamin nutrition of the sea and bacteria are significant producers and carriers of vitamin B₁₂ in the marine environment.

GENERAL FEATURES OF THE PHYTOPLANKTON

The present list of phytoplankton species includes 92 diatoms, which with Polunin's (1934) records makes a total of 114 species. Dinoflagellates are represented by 91 species, a number which may be increased still further by inclusion of the "naked" forms. Two species of Coccolithophoridae, 3 Silicoflagellata, 3 Chrysomonadineae, 2 Heterocontatae, 5 Chlorophyceae, 3 Desmidiaceae, 4 Cyanophyceae, 22 Ciliata and some unidentified Flagellata, including 6 types of cysts of unknown origin, complete the list.

Hudson Bay and Hudson Strait show a great similarity to both sides of the Atlantic, in terms of phytoplankton species, as seen from the work of Gran (1905, 1919), Gran and Braarud (1935) and Gaarder (1954). A small number of Hudson Bay species may represent relicts from a warmer period. According to Dunbar (1956), Hudson Bay, although definitely outside the subarctic waters and showing many of the characteristics of the arctic zone, should be placed in a category by itself. This is because of the high temperature and low salinity in the upper layers in summer (as high as 10°C and as low as 23‰ salinity), and because of the

preservation of warmer water relicts such as capelin and the calanoid *Acartia clausi*.

Since phytoplankton distribution is controlled also by water currents, Atlantic and northern arctic plankton find their way into Hudson Bay. The occasional visitor from warmer seas once introduced may survive under arctic conditions, but probably only in very small numbers, because of light deficiency and low temperature. Three species, *Pterosperma reticulatum*, known from Florida, the Red Sea and Newfoundland, *P. ovum*, from salps in the South Seas and from Helgoland, and *Rhabdosphaera spinosa*, from the northwest African coast and the Azores, represent possible warm water elements introduced in recent times.

The pattern of physiological adaptation of the euryhaline warm water element and freshwater autotrophs to the marine habitat is obscure. Different degrees of salinity-temperature tolerance have been specific in some arctic and cosmopolitan phytoplankton species (Smayda, 1958). The occurrence of large populations of the freshwater *Dinobryon pellucidum* and *D. balticum* in high salinities in the deeper layers of the Arctic Ocean and in Foxe Basin (author's unpublished data) indicates that freshwater forms are favoured by the low temperatures of the arctic. It is in agreement with experiments and field observations made by Doty and Newhouse (1954) that stenohaline and metahaline forms tolerate better higher salinities in low temperatures. The slow decrease of surface salinities during the ice melting period and their increase during the time of open water is thought also to be an advantageous factor in the adaptation of some freshwater species to the arctic environment.

SPECIFIC FEATURES OF THE PHYTOPLANKTON IN HUDSON BAY IN 1953*

Station 502. The horizontal net tow contained 71 species in which diatoms dominate. *Melosira islandica*, *Fragillaria gracillima*, *Botryococcus brauni*, *Pediastrum*, *Scenedesmus*, Desmidiaceae and Cyanophyceae show a strong influence of brackish freshwater elements, although the station was situated five miles from the coast. The dinoflagellates represented were *Ceratium hirundinella*, *Peridinium inconspicuum* and rare forms. It is remarkable that many freshwater Rotatoria also occurred in this haul; the typical lake inhabitant *Notholca longispina* and other freshwater species of Rotatoria were common. There were only 36 species at this station, mostly of the tycho-pelagic element.

Station 503. The net samples consisted of 67 species, both diatoms and dinoflagellates. There were no special features except for the occurrence of more diatoms at 10 m than at the surface.

Station 521. This station provided 31 species in vertical and horizontal hauls, mostly neritic and brackish species.

Station 553 (net only). This provided 28 species and showed great similarity to the previous station.

*Copies of the raw data can be obtained upon request to the author.

Stations 505, 506 and 507. These show evident dominance of *Chaetoceros compressus*, *Ch. concavicornis*, *Nitzschia closterium*, *N. seriata*, *Fragillaria nana* and other planktonic diatoms, descending to 25 m in moderate quantities. *Rhizosolenia styliformis* increased from the surface to reach 3,600 cells/l at 25 m. *Goniaulax tamarensis* was relatively numerous from the surface to 10 m, with populations of 7,680 and 8,800 cells/l. Unknown spherical forms of holozoic flagellates appeared in large numbers (41,000/l) at 10 m. *Ceratium arcticum* occurred as 1,040 cells/l at the surface, *Exuviella* sp. in small quantity only at 10 m.

Station 506. This shows a typical marine composition of species, taken in large number as deep as 50 m. Unusually great numbers of coccolithophorids (631,000), *Bodo* sp. (29,000) and a large number of unidentified flagellates occurred. *Scenedesmus* was found at 50 m only, as 2,000 cells/l.

Station 507 showed conditions similar to those at station 506.

Station 508 had poorer populations of similar composition to those at station 507.

Station 509. This produced abundant plankton, similar in composition to the stations above, with diatoms dominant. *Chaetoceros debilis* at 10 m reached a maximum of 61,560 cells/l, at 25 m showed only 3,600. *Cyclotella* sp. and *Melosira* sp. were found in relatively large quantity from the surface to 100 m. *Thalassiosira rotula* occurred as 46,000 cells/l at 25 m.

Station 510. This showed mostly diatoms, as deep as 100 m. *Chaetoceros karianus*, *Ch. concavicornis*, *Ch. atlanticus* and *Ch. debilis* were represented from the surface to 50 m by a few thousand cells per litre.

Station 512 (net tow) yielded 26 species among which *Ceratium longipes* was dominant and the littoral element common.

Station 514 showed reduced plankton, mostly diatoms among which *Chaetoceros compressus* reached 24,800, *Achnantes taeniata* 3,700 and *Thalassiosira rotula* 7,800 cells/l. There were 36 species in all, mostly diatoms and dino-flagellates.

Station 515. This showed moderately rich plankton with highest production at 25 m, mostly *Chaetoceros*, with *Thalassiosira rotula*. *Chaetoceros compressus* occurred unusually at 50 m, as 25,000 cells/l. This station showed typical pelagic communities of the area.

Station 516. Here the dominant elements were *Chaetoceros*, with 20,800 cells of *Ch. compressus* at the surface. *Thalassiosira gravida* reached 5,940 cells/l at 25 and 50 m.

Station 517. Plankton at the surface here was much reduced, and it occurred more abundantly at 10 and 25 m, where *Thalassiosira* was present as 20,400 and 5,200 cells and *Chaetoceros debilis* as 1,000 cells/l at 25 m. Freshwater and neritic elements were represented by *Fragillaria crotonensis*, Desmidiaceae, and *Coscinodiscus oculis viridis*, the latter as 1,240 cells/l at 25 m.

Station 520. Large numbers of *Pontosphaera* and unidentified flagellates occurred here - up to 100,000 cells/l. There was a maximum of *Chaetoceros* at 25 m, with *Ch. debilis* as 1,800 cells and others in relatively small numbers. In the net haul there were 59 species.

Station 521. This showed more evenly distributed plankton, the maxima however occurring in the deeper layers.

Station 522. This was remarkable in that numerical increase started at 10 m and reached, in *Chaetoceros debilis*, 200 at 10 m, 1,200 at 25 m, and 35,420 cells/l at 50 m. *Nitzschia closterium* was observed at its surface maximum at this station, with 6,220 cells/l.

Station 526 (net tow). There were nine species in the vertical haul, and 14 in the horizontal. Typical oligotrophic conditions existed.

Station 527. Poor plankton conditions prevailed here, with only 16 species being found in the sedimentation cylinders and 26, mostly neritic species, in the horizontal net haul.

Station 528 (net tow). Poor plankton, neritic and benthic forms, occurred.

Station 529. *Chaetoceros* plankton was characteristic here, with *Ch. lorenzianus* at its maximum of 27,160 cells/l at 10 m, and a population of diatoms and coccolithophorids at the surface of 183,500/l, a maximum at 10 metres of 389,000 cells/l, and a sharp decrease at 25 m.

Station 535. A small number of species occurred here in comparison with station 529. There were 48 species in the net haul.

Station 531. The horizontal net haul contained 57 species, of heterogeneous populations of neritic and pelagic diatoms and dinoflagellates.

Station 540. There were 35 species in the horizontal net haul, with a dominant *Chaetoceros* population and *Achnantes taeniata*. Dinoflagellates were abundant.

Station 544. This was one of the most productive stations, in spite of the late date. The diatom populations of *Coscinodiscus concinnus* and *Cyclotella* sp. were at their maximum, and the *Chaetoceros* group was abundant at the surface and deeper. *Nitzschia closterium* was present as 18,980, *Fragillaria nana* as 11,400 cells/l. *Leptocylindrus danicus*, found usually in small quantities, showed a population of 4,900 cells at 25 m, *Amphidinium* as 16,000, *Goniaulax tamarensis* as 11,000 and *Thalassiosira gravida* as 2,400/l. The larger population of the transition area between Foxe Channel and Hudson Strait is evident in this station, and it is also probable that these waters show a later start in their plankton increase because of inflowing arctic water bringing lower temperatures and ice. The vertical net haul at station 544 contained 32 species, the horizontal one 53 species. Various unidentified cysts were also observed.

SPECIFIC FEATURES OF THE PHYTOPLANKTON IN HUDSON BAY AND STRAIT IN 1954

Station 602. This station showed an abundant phytoplankton population, especially in the diatoms of pelagic origin. The maximum of 78,500 cells of *Chaetoceros debilis* and 210,600 *Thalassiosira* per litre was found at 3 m; there were 13,080 cells of *Thalassiosira gravida* at 15 m, 20,000 *Fragillaria* at the surface, 24,600 *Chaetoceros compressus* and 3,400 *Thalassionema nitzschioides* at 15 m, and 1,200 *Peridinium subcurvipes* at the surface. The vertical net haul contained 13 species only.

Station 603. This was still more productive, although its largest number of species was limited to the 10-metre layer: *Chaetoceros concavicornis* (12,000), *Ch. compressus* (22,400), *Ch. decipiens* (31,600 cells/l). *Ch. debilis* reached its maximum for the year with 120,000 cells at 10 m. *Ch. furcellatus* showed 100,000 at the surface, *Ch. karianus* 60,000 at 10 m, *Thalassiosira nordenskjöldi* 19,200, and *Th. rotula* 39,600 at 10 m. Freshwater species occurred as 30,000 cells/l.

Station 612. This station showed a peculiar distribution of dispersed phytoplankton populations from the surface to 100 m. At 50 m, cell numbers were: *Chaetoceros compressus* (59,800), *Ch. debilis* (34,200), *Ch. furcellatus* (48,000), *Ch. lorenzianus* (38,200). *Dinobryon balticum* and *D. pellucidum* reached 34,000/l, again showing freshwater influence. There were only 18 species in the vertical net haul, 42 and 51 species in two horizontal net hauls. Diatoms dominated in all collections.

Station 617. This showed a very rich plankton from the surface to 50 m. The greatest numbers were found here of *Chaetoceros compressus* (1,325,000 cells at 10 m), *Ch. furcellatus* (320,000 at 25 m), *Ch. socialis* (910,000 at 25 m), *Fragillaria nana* (68,000 at 25 m). Rare elsewhere, *Eucampia zodiacus* was found at its maximum of 30,000 cells/l. *Thalassiosira gravida* showed 98,000 at the surface, and 102,000 cells/l at 25 m. Of *Th. rotula* there were 55,000 cells/l at 10 m.

Station 618. This, the most easterly station discussed here, was near the east end of Hudson Strait. Populations were smaller than at station 617 because of the pelagic nature of the station. *Chaetoceros compressus* and *Ch. socialis* were taken as 353,000 cells/l at the surface.

The six phytoplankton stations located on the north side of Coats Island, in Sugluk Bay and 17 miles west of Burwell, in Ungava Bay, indicate great differences as far as composition and size of phytoplankton populations are concerned. The main species are *Chaetoceros compressus*, *Ch. furcellatus*, *Ch. lorenzianus*, *Ch. karianus* and *Ch. decipiens*, associated with *Thalassiosira gravida*, *Th. rotula* and *Fragillaria* populations.

It seems evident, comparing the 1953 and 1954 phytoplankton, that the Hudson Strait area is more fertile and productive than Hudson Bay, although the latter cannot as yet be well estimated because there are collections from only a few stations dispersed over a wide area. In July 1956 the writer observed a diatom bloom at the surface in the middle of Hudson Strait. Very dense brown patches covering a large area of several miles were observed from the bridge of H.M.C.S. *Labrador*.

QUANTITATIVE DISTRIBUTION OF DIATOMS AND DINOFLAGELLATES

The histogram in Fig. 1 shows quantitative distribution of diatoms and dinoflagellates found at the surface, 10, 25 and 50 m, in Hudson Bay (1953) and Hudson Strait (1954). It is obvious that phytoplankton populations, represented by the number of cells per litre of sea water, increase greatly when one moves from Hudson Bay towards Hudson Strait. It should be considered however that

the following factors may affect each local production: time of the sampling, distance from the coast, ice and salinity conditions, and type of the water-masses and their geographical origin. Since a single plankton station can be compared with a "single photo shot" cut from a 12-month film, our impression is greatly limited. It is therefore supposed that the production maxima are much higher in both areas, but that they were missed since they usually are of short duration. It is possible that maxima of diatoms occurred at the end of May and middle of June in Hudson Bay and later in Hudson Strait. The surface populations in June and July are small in the majority of stations as a result of lowered salinities; when salinities become higher in August and September production at the surface increases greatly. More stabilized salinity and optimal light conditions favour growth of photosynthesizing organisms, showing the highest level of vertical production. The 25-metre depth shows a decrease of plankton populations. The high number of diatoms at the 25- and 50-metre levels may represent "sinking populations" which as observed in several cases possess cysts of specific gravity greater than that of sea water. Cyst formation takes place in various species at different times of the vegetative season. Both pelagic and neritic diatoms could be carried down and up by vertical currents. Coccolithineae and other insignificant producers of biomass were not included in the histogram.

GRAZING

The main bulk of primary food in the arctic seas consists of diatoms. "The standing crop of plants at any time is the resultant balance between the rate at which they have been produced and the rate at which they have been eaten", according to Harvey (1950). This problem has attracted much attention and has been discussed from various points of view, by Fleming (1939), Riley (1946, 1953), Riley and Bumpus (1946), and others. It is generally simplified by most of the authors who put all phytoplankton in one group, and all zooplankton in the opposite one. Though zooplankton represents the main consumer of phytoplankton, reducing greatly its quantity, there are other feeders within the marine food chain represented by various taxonomic groups of holozoic and holophytic flagellates. It is of biological interest to distinguish all existing links acting in the grazing of plankton. The following groups of feeders are distinguished by the present writer:

1. Choanoflagellata, Bodonidae and many other heterophytic flagellate-ingesting bacteria, and Coccolithophoridinae.
2. Holozoic flagellates which ingest holophytic species.
3. Holophytic flagellates which ingest both holophytic and holozoic forms including copepod eggs and ciliates.
4. Ciliates, including Tinntinnidae, which feed upon diatoms and flagellates.
5. Zooplankton, which are the most efficient grazers, representing the main consumers of plants in seas.

The grazing rate of copepods is enormous. Estimates from biomass and pigment show its maximum in July and August in Greenland by Digby (1953). Harvey (1937) found 74 to 94 ml of food-bearing water per *Calanus* to be swept clear in 24 hours. Gauld (1951) found that about 70 ml per 24 hours were swept clear of *Chlamydomonas* cells. The range was from 250,000 to 2,000,000 cells.

The mean number of ciliates per litre at each station in Hudson Bay and Strait is shown in Table I. There are represented 22 species of ciliates among

TABLE I. Number of ciliates (averaged according to the number of depths sampled) taken at various stations in Hudson Bay and Hudson Strait.

Station No.	No. of ciliates	Station No.	No. of ciliates
503	350	521	615
505	420	522	1,152
506	448	527	133
507	160	529	173
508	260	535	165
509	100	544	288
510	540	549	350
514	500	602	288
515	283	603	255
516	144	612	272
517	10	617	208
520	320	618	132

which *Mezodinium*, *Laboea* and *Lohmanniella* are most common. It is supposed that these are able to make vertical migrations in search of food, because of their well developed ciliary apparatus. High numbers of ciliates are not always associated with large populations of phytoplankton which the grazers can rapidly reduce. The maximum of 1,152 ciliates at station 522 was exceptional; at most stations there were between 200 and 600 individuals per litre. Such populations can rapidly reduce the plant population.

Holophytic species of *Peridinium gargantua* (Biecheler, 1952) are voracious, and are able to ingest holophytic and holozoic flagellates. *Gyrodinium pavillardi* (Biecheler) is able to attack *Strombidium* larger than itself. Phagocytosis was observed by the author in *Massartia*, *Amphidinium* and many other genera, diatoms and various heterotrophic flagellates being captured by them. *Polykrikos* sp. is able to ingest eggs of copepods, various peridineae and flagellates. Many of the organisms have selected species upon which they feed. At Woods Hole (Elle Pond) *Prorocentrum redfieldi* was devoured mostly by Tinntinnidae (author's unpublished data). Copepods in the Point Barrow area of Alaska contained mostly dinoflagellates, while in Foxe Basin they appeared to feed exclusively upon diatoms (author's unpublished data).

QUANTITATIVE DISTRIBUTION AND ECOLOGY OF THE DIATOM SPECIES

Diatoms are the principal food producers of the arctic, where the flagellated organisms are only of minor importance. Occurrence of the diatom species is discussed below.

Achnantes taeniata Grun. Found at stations 502, 540, 555, 602 and 603, usually in small numbers in late July 1953 (2,400 to 3,700 cells/l). A truly arctic species, it is abundant among the ice floes of the Arctic Ocean and in the Baltic.

Amphiprora hyperborea Grun. Occasionally found in small numbers in both areas. Arctic, neritic.

Asterionella gracillima Grun. A freshwater species, found only at station 502, at the surface, and at station 540 in the net sample.

Asterionella kariana Grun. Rare in horizontal and vertical net hauls at stations 514, 535, 555, 602, 603, 612 and 226. This arctic neritic species was found in small quantities in the Bay of Fundy from April to September by Gran and Braarud (1935).

Atthea decora West. Taken in a net sample from station 514, this pretty benthic diatom was attached to a grain of sand as a single cell.

Asteromphalus robustus Castr. Present in net hauls at stations 540, 553, 555 and 226 in small numbers. Arctic.

Biddulphia aurita (Lyngb.) Brebisson and Godey. Common in small quantities in net and quantitative samples. As a littoral form it indicates the influence of coastal environment. Found at stations 514, 528, 531, 540, 602, 603, 612, only in horizontal net hauls. Widely distributed in the arctic coastal area.

Cocconeis placentula Ehrenb. and *Cocconeis* sp. Found attached to *Coscinodiscus concinnus* at station 502, it represents the epiphytic, littoral element.

Chaetoceros atlanticus Cleve. This oceanic species is widely dispersed over the Hudson Bay area and is also common in Hudson Strait at the majority of stations. The vertical occurrence shows that this pelagic organism forms autochthonous populations within the euphotic zone in the middle of Hudson Bay where the closed cyclonic water circulation exists. *Ch. atlanticus* disappears or is represented by very reduced populations within the littoral area. The maximum of 6,400 cells was found at 25 m at station 521, and populations were recorded from a few hundred cells to several thousand cells per litre. Occurrence from the surface to the deepest water sampled was found at stations 544, 602 and 612. It is a typical northern oceanic species, arctic and boreal, found occasionally as far south as California. Davidson (1931) found it spread over the whole of Hudson Bay.

Chaetoceros concavicornis Mang. This pelagic species is distributed in small quantities in the far northern waters of Ellesmere, Baffin and Devon Islands. It was observed by Braarud (1935) in Denmark Strait. In the Hudson Bay and Strait area it was widely distributed, represented by small populations within the coastal areas and by larger populations offshore. Its maxima were usually from 10 to 25 m, but down to 50 m at stations 509, 510 and 549, suggesting by this the probable introduction to Hudson Bay of a large population of arctic origin. The maximum of 12,000 cells/l was recorded at station 506. Large populations, continuous in vertical distribution, occurred at all stations in Hudson Strait. It is an oceanic, arctic and boreal form.

Chaetoceros convolutus Castr. This was found mostly in the net hauls. It is an oceanic, arctic and boreal form, observed in small numbers at 11 stations in Hudson Bay and Strait.

Chaetoceros constrictus Gran. This occurred mostly in net samples at stations 502, 503, 528, 531, 540 and 549, although according to Grøntved and Seidenfaden (1938) it is confined to temperate waters. It has also been found by the author at the mouth of Hudson Strait, in autumn.

Chaetoceros compressus Lauder. This is widely dispersed over the area, and was common in net hauls at stations 502, 513, 520, 526, 535, 549, 551, 553, 603 and 612. It becomes more numerous as one moves from Hudson Bay to Hudson Strait, and in Hudson Strait functions as an important producer of biomass. Counts at the surface varied from 3,620 to 325,000 cells/l. Common throughout the whole collecting period, its maximum numbers occurred in late summer.

Chaetoceros curvisetus Cl. This was found sporadically in Hudson Bay, at stations 505 at the surface (3,500 cells/l) and 544 (20,000 cells). It is an important species in subtemperate waters.

Chaetoceros diadema (Ehrenb.) Gran. Common in horizontal net samples at stations 502, 503, 514, 520, 528, 531, 535 and 603. It was not found in the sedimentation cylinders. It is possible that the maximum in Hudson Bay occurs in early spring, before sampling was begun. This neritic species is common all over the arctic.

Chaetoceros decipiens Cleve. Common in both areas in the net plankton, it occurred at station 514 at the surface as 3,640 cells/l. In 1954, at station 602, 8,000 cells/l were counted at the surface, and 1,480 at 3 m. The maximum count was 31,600 cells at station 603, where there were 12,000 at 10 m and 4,800 cells at 25 m. A large, isolated population of 28,600 cells/l was found at 10 m at station 617. It occurred often in the net samples. It is remarkable that in the Gulf of Maine the highest count recorded by Gran and Braarud (1935) was 3,600 cells/l, in August.

Chaetoceros debilis Cleve. The most common neritic *Chaetoceros* species in the area, it is an important component of the phytoplankton in northern European waters, where it is dominant in early spring. It was found in most

horizontal net hauls in Hudson Bay. According to Seidenfaden (1947) this boreal species is locally common in August in the Canadian eastern arctic, especially near the coast. Greater populations were found between Coats and Mansel Islands (stations 515, 516, 517 and 520) than in the inner part of Hudson Bay. At station 520, 12,880 cells/l occurred at 10 m, surface numbers being smaller, probably having been grazed or moved by surface wind drift. The large populations at 3 m at station 602 (78,500 cells), at the surface at station 617 (82,400 cells), and at the surface of station 618 (75,800 cells) indicate that the eastern section is the most fertile of the areas studied.

Chaetoceros densus Cleve. This was very rare in net samples, and was not observed in the sedimentation cylinders. It is an oceanic species in the Gulf of Maine, according to Gran and Braarud (1935).

Chaetoceros furcellatus Bailey. This was quite rare in the net hauls, probably because of its small size, but was taken in nets at stations 502 and 540. It occurred at the surface at station 544 as 3,620 cells/l. Larger numbers were found at station 603, where 100,000 cells were recorded at the surface and 6,200 cells at 10 m. At station 612, where it was absent at the surface, it reached a maximum of 48,000 cells at 50 m, at station 617, 14,000 cells at the surface, 10,000 at 10 m. 320,000 at 25 m, 39,000 at 50 m and 9,800 at 90 m. Sinking capacity was increased by the presence of numerous cysts.

This arctic-neritic diatom was the most abundant in Sugluk Fjord and was generally more numerous in the northern part of Hudson Bay than elsewhere in the region. It is possible that large populations which occurred in the deeper waters represented a physiological phase in which the organisms are heavier than sea water, one in which cysts are formed.

Chaetoceros gracilis Schütt. It occurred at stations 502, 520, 540, 549 and 612 in net hauls. It was found as only 160 cells/l at 50 m at station 517. Neritic-arctic, it is rather common in Hudson Strait.

Chaetoceros karianus Grun. This truly arctic species was found in net hauls at only 4 stations. It occurred at station 510 as 1,080 cells/l at the surface, and at station 549 as 6,000 cells at the surface, the latter location indicating movement southward from Foxe Basin. It is a small species which may often escape plankton nets. Found in the Kara and Barents Seas, it was recorded also by the Godthaab Expedition from West Greenland waters.

Chaetoceros laciniosus Schütt. Common at stations 503, 512, 520, 526, 527, 531, 549 and 612, in net hauls. Populations of 4,080 cells/l at the surface and 3,380 at 10 m were observed at station 507. At station 520 a few hundred per litre were found. The maximum at the depth of three m was encountered at station 602, reaching 19,600 cells. The waters at station 603 contained 42,400 cells/l at the surface, and 60,000 at 10 m. This neritic-arctic species shows a wide distribution in Greenland waters, according to Grøntved and Seidenfaden (1938).

Chaetoceros lorenzianus Grun. This species was not previously reported from the area, nor was it found in waters adjacent to Hudson Bay. The cysts and characteristic structure of *Ch. lorenzianus* were examined carefully, and they prove that the identification is correct. It occurred in net tows at eight stations. At station 506 small populations from 920 to 2,000 per litre were counted. At station 507, 16,800 were found at the surface. Smaller populations also were recorded at stations 509, 510, 514, 515, 520, 521, 522, 529 and 535. At station 544, 3,500 cells were observed at the surface. The maximum of 32,200 cells/l occurred at 5 m at station 602, where the diatom was also noticed at various depths down to 15 m. A large population of 38,520 occurred at station 612 at 50 m, an unusual find explained by the presence of cysts, and increased sinking conditions.

Chaetoceros socialis Lauder. Rare in net hauls at stations 553, 602, 603 and 612, it occurred in quantitative collections at station 617 as 300,000 cells/l at the surface, 81,000 cells at 10 m, 10,000 cells at 25 m and 1,500 cells at 50 m. Station 618, though in open waters, contained 194,000 cells at the surface, 59,600 cells at 10 m, 7,200 at 25 m and 8,000 at 50 m. Cysts were often observed. This neritic-brackish species is abundant on the coast of northern Europe. It occurs in brackish lagoons on the north Alaskan coast (author's unpublished data).

Chaetoceros septentrionalis Ostr. (Fig. 2). This species is probably more common in the region than collections indicate, but it is difficult to observe because of its small size. It occurred in horizontal net hauls at stations 502, 555 and 603.

Chaetoceros teres C. This was taken at stations 502, 531, 535, 540, 603 and 612 in net hauls. Cysts were not found. A few hundred cells per litre were recorded at station 507, and 400 cells were found at 50 m at station 535. It appeared also at station 544 in small numbers between 25 and 100 m. The maximum of 1,200 cells/l occurred at station 612 at 25 m. A temperate form, it is rare in the north.

Chaetoceros subsecundus (Grun.) Hustedt. This occurred in small numbers in the net hauls at Hudson Bay stations where cysts were observed. It is neritic on the European coast, in the Arctic Ocean and in the Mediterranean Sea (Grunow, 1884). It was observed at station 520 at 10 m as a population of 5,200 cells/l and at station 521 as a few hundred cells. The maximum of 14,360 cells was at 25 m at station 522. The maximum at the surface was found at station 544, as 10,500 cells/l, while populations of a few thousand were observed in the deeper layers. In the present state of our knowledge of the distribution of warmer-water plankton species it is not possible to classify species exactly as to their temperature requirements. It is not yet possible to distinguish between endemic species and those introduced by currents into the Bay.

Chaetoceros wighami Bright. This was occasionally found in the net hauls at stations 502, 617 and 618. It is a rare organism in Hudson Bay. According to Grøntved (1950) it is a truly arctic species. Braarud (1935) observed it in

Arctic waters east of Iceland and at the border of the Polar Current. It formed in some localities the main component of the net plankton.

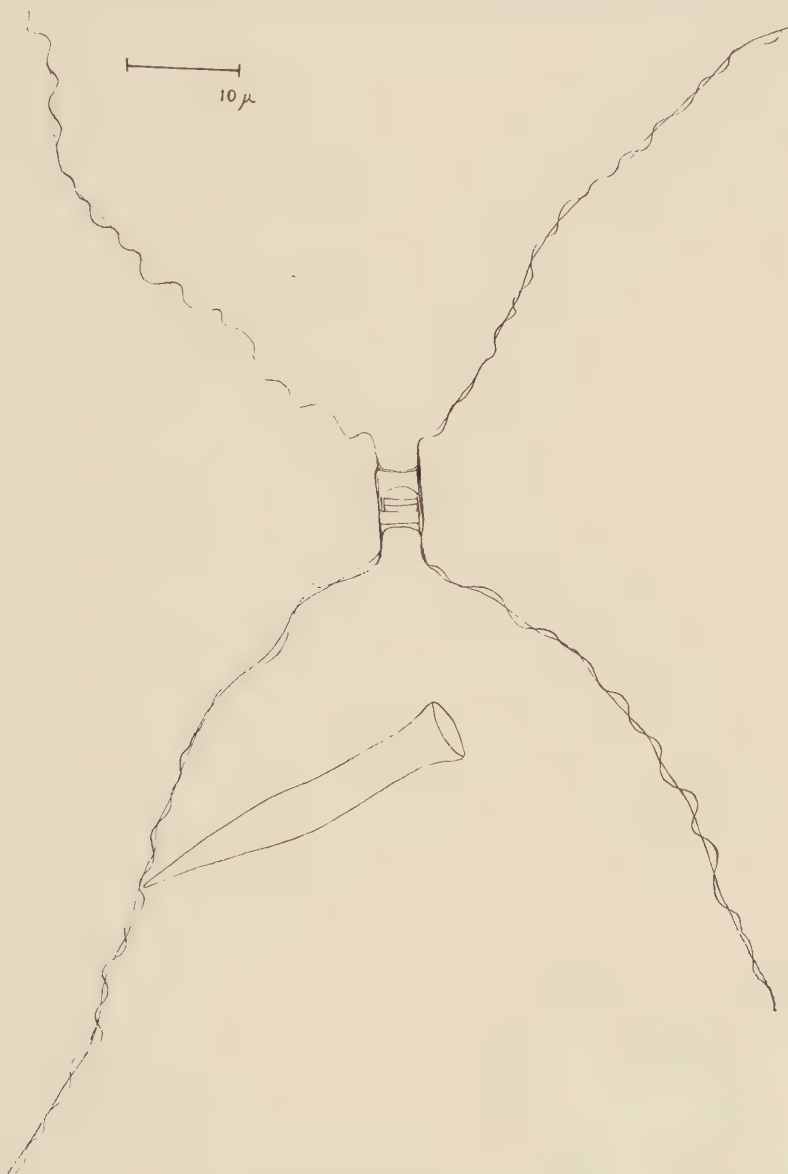


FIG. 2. *Dinobryon utriculus* epiphytic upon *Chaetoceros septentrionalis* (camera lucida).

Coscinodiscus concinnus Sm. This pelagic diatom is reported here for the first time from Hudson Bay. It was recorded previously from the eastern Canadian arctic and from the Gulf of Maine. It is common in the North Sea even in winter plankton. It is probably brought from Atlantic waters. At

station 508, 920 cells/l were recorded. At station 520, at 25 and 50 m, 360-440 cells were present. The maximum at the surface was found at station 544 as 2,000 cells/l.

Coscinodiscus oculis iridis Ehrenb. Found in oceanic plankton in all seas, it is quite common in Hudson Bay and occurred in net hauls from stations 502, 503, 540, 553 and 602. It is very common in Greenland, Cleve (1873), and occurs in immense masses in the month of May in Disko Bay, later in the year becoming scarcer (Grøntved and Seidenfaden, 1938). It is not recorded by Gran and Braarud (1935) from the Gulf of Maine. Since it usually has been found in large numbers in northern latitudes, its seasonal maximum in our area probably took place earlier than the *Calanus* samples were collected.

Coscinodiscus excentricus Ehrenb. Regularly observed by Gran and Braarud (1935) in the centrifuge samples from the Bay of Fundy and Gulf of Maine, according to Grøntved (1950) this species is as a rule considered as truly oceanic. In our observations this species occurred occasionally in net hauls but it was not observed in the sedimentation cylinders.

Coscinodiscus marginatus Ehrenb. This Atlantic species was rare in net hauls and was observed at stations 526, 540, 549 and 612. It had not been observed formerly in the Hudson Bay area, and was not reported from the Gulf of Maine. It is possible that it is brought from the Atlantic to Hudson Bay.

Coscinodiscus grani Gough. A neritic species, it was not reported previously from the eastern arctic or the Gulf of Maine. Rare in net hauls, it was found at stations 502, 512, 527, 549 and 612. It is possible that this diatom also is introduced by currents from the Atlantic. It was observed through the column of water at station 506 and had its maximum of 1,580 cells/l at 50 m. Though it occurred at many stations, represented by a few hundred cells, it is considered as a relatively unimportant organism.

Coscinodiscus lineatus Ehrenb. Known from all seas in oceanic and neritic environments, it is recorded from Norway and Denmark (Hustedt, 1930) and from the Faeroe Islands. Formerly unknown from the Hudson Bay area.

Cyclotella sp. This is probably a freshwater species, found in inshore plankton at the surface, and represented by a few hundred cells/l. The largest number of this allochthonous form was 3,000 cells/l.

Eucampia zodiacus Ehrenb. This large neritic diatom occurred in net hauls at stations 502, 540, 549 and 612. It was found at 3 stations (521, 535 and 544) discontinuously recorded through various depths in small numbers. More frequent numerically in Hudson Strait than in Hudson Bay plankton, there were 30,000 cells/l at station 617 and 13,000 at 100 m. Gran and Braarud (1935) observed it from April to June and rarely in August, but it was never abundant in the Gulf of Maine, where its maximum was 2,000 cells/l.

Fragillaria cylindrus Grun. This species was previously recorded in some samples of Nilsson from the Baffin Island coast (Cleve, 1896). Observed in net hauls from 6 stations, its vertical distribution was discontinuous, with a few

thousand cells/l, absent from the surface, at stations 503, 509 and 535. The large number of 86,000 cells/l occurred at station 617, with gradually diminishing numbers at 25, 50 and 100 m.

Fragillaria crotonensis (A. M. Edwards) Kitton. A neritic, brackish species, it was found occasionally in small numbers at 6 stations.

Fragillaria oceanica Cleve. This arctic-neritic species was observed in 2 horizontal net hauls. It is included in Gran and Braarud's (1935) list of species rare in plankton. Grøntved (1950) recorded it in the eastern Canadian arctic.

Fragillaria islandica Grun. This neritic-arctic species is represented in early diatom spring plankton, and therefore is rare in the samples collected later. It appeared at stations 502, 503, 520, 531, 555 and 549. It was not recognized in the quantitative survey. It is abundant in Hudson Strait (Polunin, 1934).

Fragillaria nana Nielsen. A temperate species, it occurred in the net plankton at stations 502, 520, 531, 540 and 553. It was seen at station 517 at the surface as only 440 cells/l and as a larger population at 10 m of 2,470 cells/l.

Leptocylindricus danicus Cleve. This was rare in quantitative samples. A temperate-boreal species, it is scattered in the Canadian eastern arctic (Grøntved, 1950), and very abundant north of Europe. Gran and Braarud (1935) found a maximum of 5,000 cells/l in Passamaquoddy Bay.

Navicula vanhoffeni Gran. Observed at 8 stations, it seems to be distributed over the whole area in small numbers. It is an arctic form.

Navicula sp. A small, neritic form, this occurred at coastal stations in net hauls and sedimentation cylinders as populations of a few hundred cells per litre.

Nitzschia frigida Grün. Recorded on a few occasions in horizontal net hauls, it is a truly arctic neritic form, mostly attached to sand or mud particles.

Melosira arctica Dickie. This species was observed by Ross (1947) as a typical ice diatom, in the ice or attached to the ice, in early spring. Recorded as 5,800 cells/l at the surface at station 529, it occurred in small numbers only at stations 503 and 515.

Melosira islandica Müller. This freshwater species was found mostly in horizontal net hauls, and was dominant at stations 502 and 514, rare at stations 531 and 612. Its maximum was at station 509, as 1,560 and 1,300 cells/l at 25 and 50 m.

Melosira nummuloides (Dillw.) Ag. It occurred only at station 502, in net plankton.

Nitzschia delicatissima Cleve. This widely distributed species, according to Gran and Braarud (1935), may be regarded as oceanic, although it is often abundant in inshore waters. According to Grøntved (1950) it is a temperate species, presumably coming to our area only with northward moving water in the autumn. It was not reported previously from Hudson Bay. This shows a very limited occurrence at stations 506, 514 and 527.

Nitzschia closterium Sm. This occurs frequently in the plankton, and was recorded over the whole area in eight hauls. It is more common than other species of the genus and has continuous vertical distribution at 6 stations. The maximum found was 18,980 cells/l at 25 m at station 544 in Foxe Channel. A smaller population of this diatom (13,000 cells) occurred at the surface. It is remarkable that quantitative fluctuations of this diatom in the majority of samples was within a few hundred cells.

Nitzschia seriata Cleve. This is a common species, often associated with *N. closterium*. Polunin (1934) found it to be rare in Hudson Strait, Davidson (1931), wide-spread in Hudson Bay, but "in very small numbers". Grøntved suggested that it is probably most common early in the year. It is a northern to arctic neritic species, present at Scotch Cap, Alaska (Cupp, 1943), and recorded by Gran (1912) as an arctic, oceanic species. Populations were small in Hudson Bay, with a maximum of 2,400 cells/l. It was more common in Hudson Strait stations, its maximum of 10,000 cells occurring at station 617, at 25 m.

Podosira glacialis (Grun.) Jorg. Found frequently in Hudson Strait in 1953, it is reported here for the first time from Hudson Bay. Gran and Braarud (1935) consider it as a typical spring form. It was observed at stations 502, 520 and 553 in net hauls; otherwise 200 cells/l occurred at station 612 at 10 m.

Rhizosolenia styliiformis Brugh. It is rare in Hudson Strait, Polunin (1934) and Davidson (1931) reporting it from Hudson Bay. It occurred over the whole area in net hauls and in very scattered populations of a few hundred cells/l at 12 stations.

Rhizosolenia hebetata f. *hiemalis* Gran. This occurred only in the net hauls as a very rare form. A true "autumn type" in the eastern Canadian arctic (Grøntved), it was never abundant in the Gulf of Maine (Gran and Braarud, 1935).

Rhizosolenia hebetata f. *semispina* (Hensen) Gran. An Atlantic species, it was found only in the net plankton at stations 502, 503, 520 and 540 and is regarded as a late autumn species.

Rhizosolenia imbricata var. *schrubsolei*. This oceanic species was found in horizontal plankton samples, at stations 512, 514, 520 and 528, in small quantities.

Rhizosolenia fragillissima Bergon. This neritic species was found in the net plankton only at stations 502 and 531. Not reported formerly from Hudson Bay, it is known from the Gulf of Maine.

Sceletonema costatum (Greville) Cleve. This neritic-boreal species was found only in net hauls at stations 520, 531, 535 and 549, and was not seen in the sedimentation cylinders. It probably belongs to the Atlantic-neritic group which, although they may occur in Hudson Bay, appear not to propagate satisfactorily there and so do not become important in the phytoplankton. The species was common in the October plankton of the Godthaab Expedition. In the Gulf of Maine its maximum is in the warmest season (Gran and Braarud, 1935).

Stephanodiscus astrea (E.) Grun. This freshwater species occurred mostly in net samples, being observed in small numbers at stations 502, 520, 521 and 540. It has not been reported before from Hudson Bay.

Surirella sp. Present at stations 502, 520 and 551, it is a benthic freshwater diatom, observed only as single cells.

Thalassionema nitzschioides Grun. This eurythermic and cosmopolitan species (Smayda, 1958) was observed in six horizontal net hauls. It was not abundant. Maximum numbers occurred at station 612, where 8,360 cells/l were found at the surface, and also at 25 m. Gran and Braarud (1935) found it dispersed over the whole area of the Gulf of Maine from April to September with numbers up to 100,000/l.

Thalassiothrix longissima Cleve and Grun. This large, oceanic species, considered also as an arctic-boreal or north temperate species, was rare in the net hauls as far as the number of individuals was concerned, but it had a wide distribution at stations 514, 520, 531, 535, 549, 551, 553 and 612.

Coscinosira polychorda Gran. A neritic north temperate species, it is widely distributed in the arctic (Cupp, 1937, 1943). It was occasionally found in small quantities in the net plankton. Its maximum, at 10 m, reached 3,600 cells at station 603, and 2,620 at 50 m at station 544.

Thalassiosira decipiens Grun. Joerg. This neritic, north temperate species was rare in the net hauls, taken at only a few stations. In European waters it has a similar distribution; as in the Gulf of Maine it is very common, but never abundant. It usually is relatively prominent in the plankton in winter and probably has a slow rate of propagation and relatively low light requirements (Gran and Braarud, 1935).

Thalassiosira subtilis (Ostenf.) Gran. This was observed by Polunin (1934) in the Hudson Strait area and was considered as a common species. It was found in the net plankton samples, where it occurred at 8 stations. At station 517 a population of 4,800 cells/l was found.

Thalassiosira gravida Cleve. This species occurred in small and discontinuous populations, which are significant in the total phytoplankton production in Hudson Bay. Its maxima of 98,000 cells/l at the surface and 102,000 at 25 m were found at Sugluk (station 617) in Hudson Strait. Smaller populations of this organism occurred within the neritic area of Evans Strait, close to Coats Island, continuously distributed vertically. It was considered by Gran (1912) as an arctic neritic form.

Thalassiosira rotula Meunier. This species appeared at all stations. It is considered as a significant producer of biomass and food, because of its large size. Continuous vertical occurrence was observed at stations 509, 510, 516, 517 and 549 in varying numbers from a few thousand to over 20,000 cells/l. The maximum at the entrance to Hudson Bay occurred at 25 m at station 602 where it reached 210,600 cells/l. The numerical increase of this diatom towards Hudson Strait

is well marked by its continuous vertical distribution. The maximum in Hudson Strait was found at station 617 at the surface, represented by 220,000 cells/l. It was considered by Polunin (1934) as a temperate visitor in autumn. Grøntved and Seidenfaden (1938) called its appearance in Hudson Strait "peculiar" since it was regarded as a southern temperate form.

Occurrence of fairly large populations of *Th. rotula* in the northernmost part of Foxe Basin (unpublished data) indicate that it is a form well adapted to severe arctic conditions and that it is probably indigenous to those waters. Whether such populations originated from the Atlantic stock cannot be established yet. It was not however recorded in the Gulf of Maine by Gran and Braarud. The distributional pattern of *Th. rotula* is not established yet in the arctic waters. Cupp (1937) defines it as a neritic, temperate and south temperate species, moderately common off southern California. Present in the Gulf of California and north to Scotch Cap, Alaska, *Th. rotula* was found also in phytoplankton of the coastal waters of Point Barrow (unpublished data), but in net plankton only. Populations in arctic waters are supposedly introduced from the Pacific and Atlantic by currents. Factors controlling the discontinuous distribution of this diatom are still obscure.

The benthic diatoms were fairly common in the net and reverse microscope samples. They are not adapted to the floating life in plankton owing to their heavy membranes and secreted mucus serving for attachment to solid substrate. They are introduced to plankton in turbulent or stormy waters. The more common forms were *Gyrosigma spenceri*, *Gyrosigma* sp., *Grammatophora marina*, *Isthmia nervosa*, *Licmophora abbreviata*, *Melosira nummuloides*, *M. arenaria*, *Navicula* sp., *Pleurosigma* sp., *Pinnularia* sp., *Rhabdonema arcuatum*, *Cocconeis placentula*, *Cymbella* sp., and *Surirella* sp.

QUANTITATIVE DISTRIBUTION AND ECOLOGY OF THE DINOFLAGELLATE SPECIES

These forms have received little attention in northern waters. Calkins (1901) reported them from Nova Scotia, and Gran (1919) recorded more common forms from the Gulf of St. Lawrence. Martin (1929) found some new species in non-arctic marine and brackish habitats. Gran and Braarud (1935) contributed to our knowledge of the Gulf of Maine. Seidenfaden (1947) made a list of dinoflagellates from the Canadian arctic. The distribution of *Ceratium* sp. in the Newfoundland area was studied by Frost (1938). Many new species were described by Gaarder (1954) from the Atlantic area. Holmes (1956) studied the quantitative dynamics of dinoflagellates in the Labrador Sea. Experiments by Barker (1935), Braarud (1945) and others show the dinoflagellates are a warm water group. The absence of many thecate species in the arctic allows us to conclude that low temperature and dim arctic light do not favour them.

Sixty-two species were found in the Hudson Bay and Hudson Strait material. In a special survey of dinoflagellates, 41 more species were found in Hudson Bay and Hudson Strait (unpublished data). The so-called "naked" dinoflagellates

which are deformed or burst after fixation cannot be identified properly in preserved material.

Genus *Ceratium*. The most common species in the *Calanus* samples were *C. arcticum* and *C. longipes*. *C. tripos* was less common and *C. hirundinella* occurred only once in a net haul, indicating freshwater influence from the Churchill River. *C. macroceros* and *C. bucephalum* were found mostly in the Hudson Strait area. The rare *C. karsteni*, from station 618, seems to be an Atlantic species. It is remarkable that *C. fusus*, *C. lineatum* and *C. furca*, common in the Atlantic and at Point Barrow, Alaska, were entirely absent from the *Calanus* collections. All *Ceratium* species were represented by small populations, except at station 505, where 1,040/l were counted from 10 m. Frost (1938) considered *Ceratium* species as indicators of hydrographic conditions in Newfoundland waters. No similar use could be made of the material treated here because of the infrequent occurrence of the species.

Goniaulax tamarensis, studied by Braarud (1945) and Gaarder (1954), was common at many stations, where numbers ranged from a few hundred to 11,000 cells/l (the latter at station 544). The species was found ingested by *Ptychocylis*, *Parafavella*, *Tintinnopsis* and other ciliates. Focal pellets containing *G. tamarensis* indicate that some unidentified crustaceans can feed selectively on *Goniaulax*, and suggest that such grazers are able to reduce considerably populations of the genus. Paralytic shellfish poisoning has been associated with *G. tamarensis* in certain parts of the Bay of Fundy where it constitutes the food of molluscs (Needler, 1949).

COCCOLITHOPHORIDINEAE, SILICOFLAGELLATAE, CHRYSOMONADINEAE, BODONIDEAE AND MINOR GROUPS OF FLAGELLATES

Although the taxonomic identification of Coccolithophoridae cannot be done suitably with the light microscope, an effort was made to identify some of the organisms and to count them. *Coccolithus huxleyi* was fairly common in Hudson Bay, populations occurring mostly at the surface and at 10 m, probably because of higher temperatures in the upper water layers. Numbers at station 507 were outstanding, reaching 1,438,000 cells at the surface and 480,000 cells/l at 10 m. At station 506, 631,000 at the surface and 63,000 cells/l at 10 m were found. Smaller numbers were found in Hudson Strait.

Distephanus speculum (Ehrenb.) Heckel. This organism, abundant in warm seas, including European waters (Gran, 1915), was very rare in this material. Another silicoflagellate, *Ebria tripartita* (Schum.) Lemmermann, also common in boreal waters, occurred only twice in the net hauls.

Bodo sp. A small holozoic form with two uneven flagella occurred at station 503, represented by a population of 3,500 cells/l. The greatest number was found at station 549, as 29,000 cells/l. This organism is not identical to the species of *Bodo* found by Braarud and Bursa (1939) in Oslo Fjord.

Dinobryon balticum (Schütt) Lemmermann. Common in fresh and brackish waters of Europe, this species was found at Point Barrow, Alaska, in larger numbers and at different depths than in Hudson Bay (author's unpublished data). *D. balticum* and *D. pellucidum* can adapt themselves to euryhaline habitats during the melting period of arctic ice and then become mixed with the brackish surface and deeper water of high salinity. The intrusion of freshwater microflora into the marine environment is associated with river influence and ponds of melting ice found abundantly in summer over the arctic area. The contrast in occurrence of *Dinobryon* in Hudson Bay (station 507) and Hudson Strait (stations 600, 612, 617 and 618) is shown in Table II.

TABLE II. *Dinobryon* occurrence in Hudson Bay (station 507) and in Hudson Strait (stations 600, 612, 617 and 618).

Depth	Station				
	507	600	612	617	618
m.					
0	9,000	30,000	17,000	11,000	38,400
10	—	3,900	34,000	8,000	31,200
25	—	40,200	3,500	17,600	2,500
50	—	—	—	1,200	—

Dinobryon pellucidum Levander. This was less common than *D. balticum*. It is fairly common in Greenland waters, according to Grøntved and Seidenfaden (1938).

Dinobryon utriculus Stein. This is another rare freshwater organism which has not been reported formerly from brackish or marine waters. Only a few specimens were seen in a net sample from station 529. One of them was attached to the diatom *Chaetoceros septentrionalis* (Fig. 2), such an epiphytic phase indicating that the small population was introduced into the sea from fresh water.

REMARKS ON TAXONOMY OF SOME RARE AND UNKNOWN SPECIES

Pterosperma reticulatum Ostenf. (Fig. 3). Spherical cells with a hexagonal membrane reticulum. Protoplasm dense, containing yellow pigment indicating that *Pterosperma* is of phylogenous origin and related to the Heterocontae. Specimens from Canadian waters are identical to those from the Red Sea (Ostenfeld and Schmidt, 1901, after Gaarder, 1954). Specimens from Florida were 80 to 100 μ and had fewer polygons, from north of Spain and east of Newfoundland 30 to 77 μ (Gaarder, 1954).

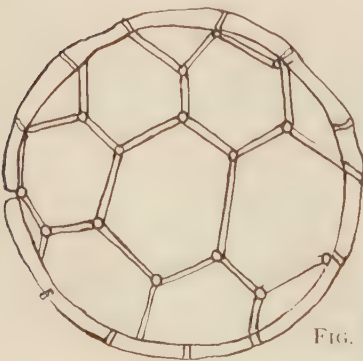


FIG. 3. *Pterosperma reticulatum* (camera lucida, $\times 2400$).

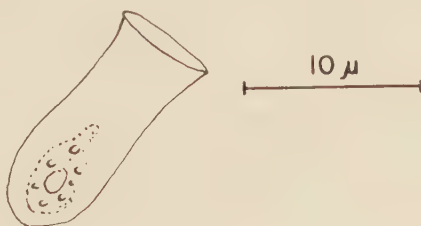
Pterosperma ovum Gaarder. This form was described by Gaarder (1954) from south of Ireland, and several specimens were also collected off Cape Finisterre (Spain). As far as general morphological features are concerned, specimens here are almost identical to the descriptions and drawings of Gaarder (1954, fig. 19a, b), except for size, the Hudson Bay cells being larger. The cell diameter of Gaarder's specimens was 28 to 46 μ , including lamellae 55 to 62 μ ; in the Hudson Bay material length, including lamellae, is 230 μ , breadth 100 μ , length of the cell, without lamellae, 125 μ . The large size of the Hudson Bay specimens therefore puts them closer to Lohmann's *P. ovum hispidum gigas* (1904, p. 31, pl. V, fig. 7) from the Florida Current (after Gaarder, 1954). Lohmann's specimens, with a diameter of 390 μ , have branching protuberances separated at the base, shorter than in the Hudson Bay form. Gaarder supposed that *P. ovum hispidum gigas* might be identical to Stein's "cysts of *Cladopyxis brachiolata*" (1883, p. 19, pl. II, fig. 12, 13) from Helgoland, and others found in salps in the South Seas, specimens in which the branching protuberances may have a continuous film at the base. The Hudson Bay form is closely related to the fossil *Hystrichosphaera* spp., especially *H. ramosa* (Ehrenberg) and *H. wetzel* (Deflandre, 1952, p. 324, fig. 17).

Rhabdosphaera spinosa Gaarder. Spheroid and subspheroid cells were found at station 603. They are similar to but smaller than previously described specimens. Some contained brown or green pigment, indicating the holophytic origin of the organism. The numerous spines were of uneven size, about 2 to 4.5 μ in length. The cell membrane was bi-contoured and thick. Length of the subspheroid cells was from 18 to 20 μ , breadth from 11 to 13 μ , while Gaarder's (1954) specimens were from 30 to 45 μ . Elsewhere the species is known along the northwest African coast and in the area between the Azores and the Sargasso Sea.

UNIDENTIFIED EPIPHYTIC CHRYSOMONADINEAE

A small, probably holozoic epiphytic chrysomonad, with protoplasm enclosed within the tubular membrane, open at the top, wider than the base, is shown in Fig. 4. The shrunken protoplasm contains a nucleus and some products of

FIG. 4. Lorica of an unidentified chrysomonad (*camera lucida*, $\times 2400$).



metabolism. It was attached to the bottom of the tube-shaped membrane. Some free and floating individuals were found, attached to a diatom, at station 503. It is possible that these organisms came from a river, together with the

diatoms upon which they grew. Dimensions are: length of the membrane, $15\ \mu$; breadth of the apex, $6\ \mu$; breadth of the attachment, $4.5\ \mu$.

Polyasterias problematica (Cleve) Meunier. This enigmatic organism (Fig. 5), recorded from the middle Baltic by Rumek (1948) and others, was studied more recently by Erdtmann (1954) and Gaarder (1954). *Polyasterias* was found commonly in horizontal plankton hauls at stations 553 and 603. Most specimens possessed 6 hyaline arms, symmetrically disposed, with broadened and serrated ends around the spherical cell in the centre. There were also 7-, 8- and even

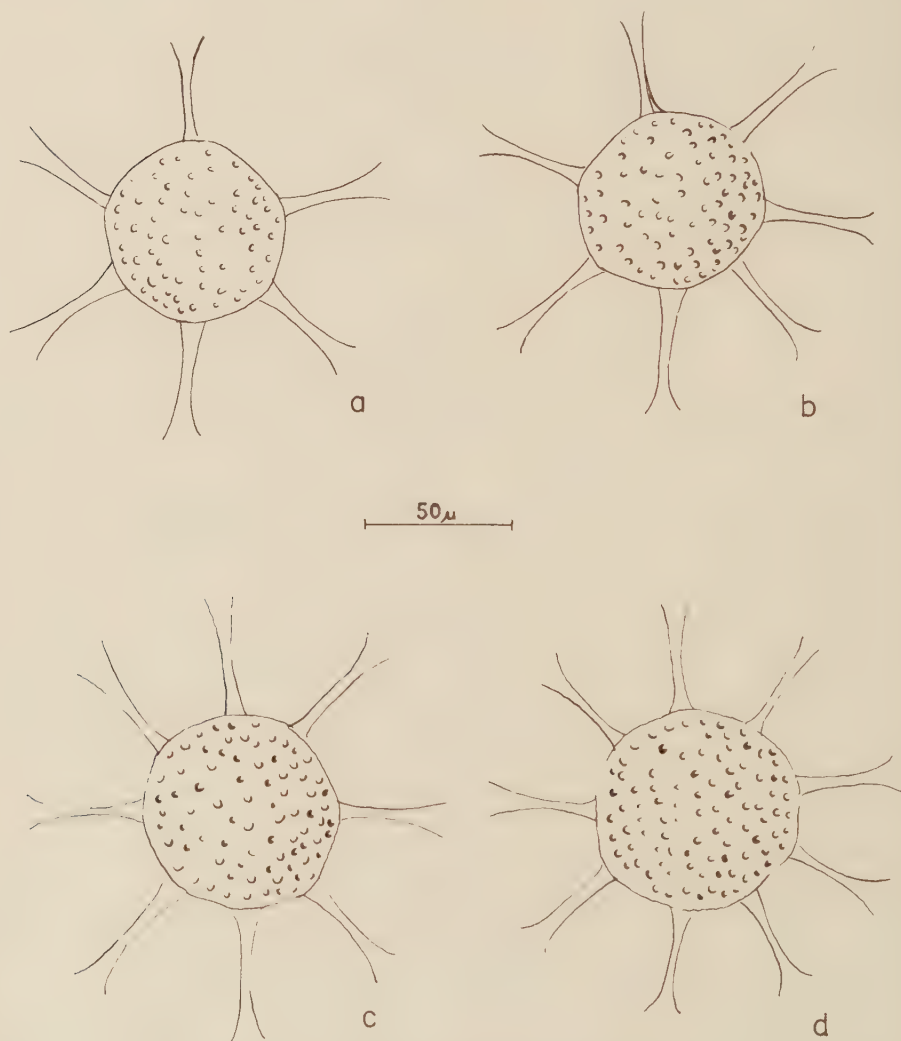


FIG. 5. *Polyasterias problematica* (camera lucida). a, 6-armed; b, 7-armed; c, 8-armed; and d, 9-armed forms.

9-armed specimens, all quite rare. Gaarder (1954) found specimens with 5 protuberances, and one with 6, off Cape Finisterre (Spain) and south of the Azores.

The author's observations in the Baltic (unpublished data), carried out on live *Polyasterias*, showed that small and larger colourless swimmers are formed inside small cells, liberated probably through the openings found within the arms. Since the organism is rare, the origin of the individuals with varying numbers of protuberances is unsolved. Dimensions of the Hudson Bay specimens: length of the arms, 32 to 40 μ ; diameter of central cell and arms, 150 μ . Occurrence elsewhere is the Baltic, Atlantic, North Sea, Skagerrak.

Unknown flagellate cysts (Fig. 6a, b). These were observed at stations 603, 528 and 502. Figure 6a shows a cyst with well defined pores. The membrane was sculptured with delicate dots in regular order. Small spines were observed

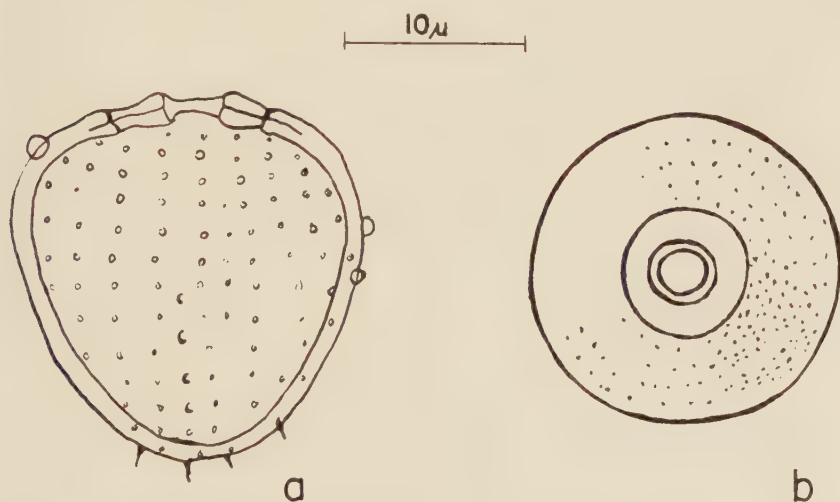


FIG. 6. Cyst of an unidentified flagellate (*camera lucida*, $\times 2400$). *a*, side view; *b*, front view, showing the apical pore.

on the posterior part of the cyst. The membrane was bright yellow. The colourless protoplasm with reserve materials and nucleus indicates the holozoic nature of the cyst-forming organism. The cyst in apical view (Fig. 6b) shows a round pore opening surrounded by a wide outside and narrow inside ring. Length was 28 μ , breadth 12 μ . The specimen figured was taken at station 528 on August 9, 1953.

Other cysts of unidentified flagellates were observed at station 549 in small numbers in horizontal net hauls in September 1953. Figure 7a-c shows cysts with large wrinkled membrane collars, with the irregular folds of the collar

membrane running excentrically. The spherical cell had a yellow-brown membrane in which small and large grains of reserve materials were observed. The surrounding hyaline membrane varied from 6 to 14 μ .

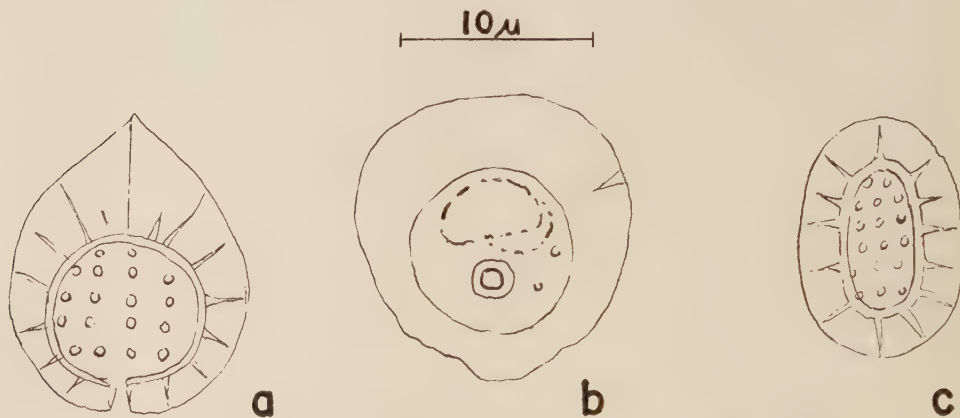


FIG. 7. Cyst of an unidentified flagellate (*camera lucida*, $\times 2400$). *a*, lateral view; *b*, front view, showing apical pore; *c*, side view.

OCCURRENCE OF SPECIES IN THE VERTICAL AND HORIZONTAL NET HAULS

While even the finest plankton nets cannot be used for accurate estimation of phytoplankton biomass, because of loss of the smallest organisms through the net meshes, net tows may be extremely useful in supplementing the relatively small quantitative collections to give increased qualitative results. A fairly short net tow will sample many hundreds of times the water volume of one quantitative collection taken from a closing bottle (and examined with the inverted microscope), and thus increase greatly the chance of collecting the rarer organisms. As an example of this, station 502 (5 miles northwest of Churchill) yielded 33 species according to the inverted microscope examination, and 39 additional species in the net tow. In this group 16 marine diatoms and 8 dinoflagellates were autochthonous, while 12 species, like *Asterionella gracillima*, *Gomphonema* sp., Cyanophyceae, Desmidiaceae and green algae showed a freshwater origin.

Coexistence of Atlantic, arctic and freshwater forms was noticed on a few occasions in the *Calanus* samples of 1953 and 1954. This feature was most apparent in the clearly mixed waters of Hudson Strait. The number of species in autochthonous populations in strictly arctic water appears to be smaller than in areas where various water types are mixed (e.g. arctic and Atlantic). This is shown clearly by the genus *Ceratium*. In the mixed waters of northern Hudson Bay 7 species of *Ceratium* were found, while in the arctic waters of Foxe Basin (author's unpublished data) 2 species were recorded, *C. arcticum* and *C. elongatum*, the only true arctic forms of the genus.

TABLE III. Diatoms found in Hudson Bay and Hudson Strait.

<i>Achnantes taeniata</i> Grunow	<i>Fr. islandica</i> Grunow
<i>Amphiprora hyperborea</i> Gran	<i>Gyrosigma spenceri</i> Cleve
<i>Asterionella kariana</i> Grunow	<i>Grammatophora marina</i> Cleve
<i>A. gracillima</i> Heib.	<i>Isthmia nervosa</i> Kützing
<i>Asterolampra</i> sp.	<i>Leptocylindricus danicus</i> Cleve
<i>Attheya decora</i> West	<i>L. minimum</i> Gran
<i>Bacteriosira fragilis</i> Gran	<i>Licmophora abbreviata</i> Agardh
<i>Biddulphia aurita</i> Brebisson & Goday	<i>Melosira arenaria</i> Moore
<i>Chaetoceros atlanticus</i> Cleve	<i>M. arctica</i> Dickie
<i>Ch. borealis</i> Bailey	<i>M. islandica</i> Karsten
<i>Ch. concavicornis</i> Gran	<i>M. nummuloides</i> Agardh
<i>Ch. convolutus</i> Castracane	<i>Melosira</i> sp.
<i>Ch. compressus</i> Lauder	<i>Navicula distans</i> Smith
<i>Ch. constrictus</i> Gran	<i>N. vanhoffeni</i> Gran
<i>Ch. curvisetus</i> Cleve	<i>Navicula</i> sp.
<i>Ch. decipiens</i> Cleve	<i>Nitzschia closterium</i> Smith
<i>Ch. debilis</i> Cleve	<i>N. delicatissima</i> Cleve
<i>Ch. eibeni</i> Grunow	<i>N. pungeus</i> Gran
<i>Ch. furcellatus</i> Bailey	<i>N. seriata</i> Cleve
<i>Ch. diadema</i> Ehrenberg	<i>N. frigida</i> Grunow
<i>Ch. gracilis</i> Schütt	<i>Porosira glacialis</i> Jörgensen
<i>Ch. lorenzianus</i> Grunow	<i>Pleurosira</i> sp.
<i>Ch. lacinosus</i> Schütt	<i>Pinnularia</i> sp.
<i>Ch. teres</i> Cleve	<i>Rhabdonema arcuatum</i> Kützing
<i>Ch. septentrionalis</i> Oestrup	<i>Rhizosolenia alata</i> Brightwell
<i>Ch. socialis</i> Lauder	<i>Rh. styliformis</i> Brightwell
<i>Ch. karianus</i> Grunow	<i>Rh. styliformis</i> v. <i>shrubsolei</i> Gran
<i>Ch. wighami</i> Brightwell	<i>Rh. styliformis</i> v. <i>hebetata</i> Gran
<i>Chaetoceros</i> sp.	<i>Rh. fragillissima</i> Bergon
<i>Cocconeis placentula</i> Ehrenberg	<i>Sceletonema costatum</i> Cleve
<i>Coscinosira polychorda</i> Gran	<i>Stephanopyxis nipponica</i> Gran & Yendo
<i>Coscinodiscus concinnus</i> Smith	<i>Surirella</i> sp.
<i>C. oculis iridis</i> Ehrenberg	<i>Actinoptychus undulatus</i> Ralfs
<i>C. grani</i> Gough	<i>Thalassiosira bioculata</i> Ostenfeld
<i>C. marginatus</i> Ehrenberg	<i>Th. gravis</i> Cleve
<i>C. lineatus</i> Ehrenberg	<i>Th. hyalina</i> Gran
<i>Coscinodiscus</i> sp.	<i>Th. nordenskjöldi</i> Gran
<i>Stephanodiscus astrea</i> Grun.	<i>Th. rotula</i> Meunier
<i>Eucampia zodiacus</i> Ehrenberg	<i>Th. subtilis</i> Gran
<i>Fragillaria cylindricus</i> Grunow	<i>Th. decipiens</i> Jörgensen
<i>Fr. striatula</i> Lyngb.	<i>Thalassiosira</i> sp.
<i>Fr. crotonensis</i> Kitton	<i>Thalassionema nitzschioides</i> Grun
<i>Fr. nana</i> Nielsen	<i>Thalassiothrix frauenfeldti</i> Grunow
<i>Fr. oceanica</i> Cleve	<i>Th. longissima</i> Cleve & Grunow

TABLE IV. Dinoflagellates found in Hudson Bay and Hudson Strait.

<i>Amphidinium</i> sp.	<i>P. conicum</i> Ostenfeld
<i>Glenodinium lenticula</i> Schiller	<i>P. crassipes</i> Kofoid
<i>Glenodinium</i> sp.	<i>P. curvipes</i> Ostenfeld
<i>Goniodoma polyedricum</i> Jörgensen	<i>P. denticulatum</i> Gran & Braarud
<i>Goniaulax catenata</i> Kofoid	<i>P. depressum</i> Bailey
<i>G. spinifera</i> Claparède & Lachmann	<i>P. divergens</i> Ehrenberg
<i>Goniaulax</i> sp.	<i>P. obtusum</i> Karsten
<i>Exuviella baltica</i> Lohmann	<i>P. leonis</i> Pavillard
<i>Ceratium arcticum</i> Cleve	<i>P. pallidum</i> Ostenfeld
<i>C. bucephalum</i> Cleve	<i>P. pentagonum</i> Gran
<i>C. longipes</i> Gran	<i>P. curvipes</i> Ostenfeld
<i>C. macroceros</i> Cleve	<i>P. subcurvipes</i> Lebour
<i>C. tripos</i> (Mueller) Nitzsch.	<i>P. oceanicum</i> Vanhoffen
<i>C. lineatum</i> Cleve	<i>P. trochoideum</i> Lemmermann
<i>C. karsteni</i> Jörgensen	<i>P. thorianum</i> Paulsen
<i>Ceratium</i> sp.	<i>P. triquetrum</i> Lebour
<i>Dinophysis acuminata</i> Claparède & Lachmann	<i>P. grani</i> Ostenfeld
<i>D. acuta</i> Ehrenberg	<i>P. brevipes</i> Paulsen
<i>D. grani</i> Paulsen	<i>P. islandicum</i> Paulsen
<i>D. islandica</i> Paulsen	<i>P. roseum</i> Paulsen
<i>D. arctica</i> Broch	<i>P. finlandicum</i> Paulsen
<i>D. norvegica</i> Claparède & Lachmann	<i>P. steini</i> Jörgensen
<i>D. robusta</i> Braarud (cysts)	<i>P. subinermis</i> Paulsen
<i>Oxytoxum gladiolus</i> Stein	<i>P. mite</i> Pavillard
<i>Peridinium avellana</i> Leb.	<i>P. globulus</i> Stein
<i>P. minusculum</i> Pavillard	<i>Prorocentrum reticulatum</i> Bütschli
<i>P. achromaticum</i> Levander	<i>Phalacroma rotundatum</i> Clap. & Lachm.
<i>P. cerasus</i> Peters & Smith	<i>Ph. rudi</i> Braarud

TABLE V. Flagellates, algae, desmidiaceans and cyanophyceans found in Hudson Bay and Hudson Strait.

<i>Dinobryon pellucidum</i> Levander	<i>Trochiscia</i> sp.
<i>D. balticum</i> (Schütt) Lemmermann	<i>Scenedesmus quadricauda</i> Brebisson
<i>Coccolithus huxleyi</i> Kamptner	<i>Peridinium ovatum</i> Schütt
<i>Coccolithus</i> sp.	<i>P. simplex</i> Lemmermann
<i>Distephanus speculum</i> Haeckel	<i>Aphanizomenon flos-aquae</i> Ralfs
<i>Ebria tripartita</i> Lemmermann	<i>Gomphonema</i> sp.
<i>Bodo</i> sp.	<i>Anabaena</i> sp.

TABLE VI. Ciliates found in Hudson Bay and Hudson Strait.

<i>Laboea acuminata</i> Leegaard	<i>Tintinnus acuminatus</i> Jörgensen
<i>L. reticulata</i> Leegaard	<i>T. norvegicus</i> Dady
<i>L. strobila</i> Lohmann	<i>Leptotintinnus bottnicus</i> Jörgensen
<i>L. spiralis</i> Leegaard	<i>Tintinnopsis beroidea</i> Jörgensen
<i>L. conica</i> Lohmann	<i>T. parvula</i> Jörgensen
<i>Didinium gargantua</i>	<i>T. karajakensis</i> Brand
<i>Ptychocylis urnula</i> Brandt	<i>Tintinnopsis</i> sp.
<i>P. obtusa</i> (Brandt) K. & C.	<i>Codonella</i> sp.
<i>P. arctica</i> (Brandt) K. & C.	<i>Stenosomella ventricosa</i> Jörgensen
<i>P. media</i> (Brandt) K. & C.	<i>Undella</i> sp.
<i>P. gigantea</i> Kofoid & Cleve	<i>Woodania conicoides</i> Leegaard
<i>Ptychocylis</i> sp.	

ACKNOWLEDGMENTS

The author wishes to give special thanks to Dr M. J. Dunbar, of McGill University, with whose help this study was begun in 1954 with the support of a Carnegie Arctic Scholarship of the McGill-Carnegie Arctic Program.

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The Quality of Fish Flour, Liver Meal, and Visceral Meal as Sources of Dietary Protein^{1,2}

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ABSTRACT

Rats were used to test the digestibility and protein quality of dried preparations of muscle and viscera from cod and haddock, and of liver from cod.

The digestibility of the preparations from muscle and viscera was good, and better than that of the preparation from liver.

The metabolic utilization of nitrogen and the support of growth were good in the case of the muscle preparation, and poor in the case of the visceral and liver preparations.

INTRODUCTION

PREPARATIONS OF FISH MUSCLE have been used in feeding experiments with rats, in some cases to supply all of the dietary protein (Drummond, 1918; Kik and McCollum, 1928; Lanham and Lemon, 1938; Nilson *et al.*, 1947; Beveridge, 1947; Morrison and Campbell, 1960), and in others to supplement cereal protein (Kik and McCollum, 1928; Sure, 1957; Morrison and Campbell, 1960). Observations on the growth and studies of the nitrogen metabolism have in all cases produced evidence that these proteins are among the best in nutritional quality.

At the Fisheries Research Board of Canada Technological Station in Halifax, a dry, fat-free preparation of fish muscle has been made, which is called fish flour (Guttmann and Vandenheuvel, 1957). It is 15.0 to 15.7% nitrogen on a dry, fat-free basis, but there is 2 to 3% residual moisture and 2 to 5% ash. The sample which we tested was 14.4% nitrogen, which corresponds to 90% crude protein. Its amino acid composition is known (Guttmann and Vandenheuvel, 1957), and it has been shown to be of high nutritional quality (Morrison and Campbell, 1960). It has been made from cod and haddock filleting trimmings, a cheap source material that can be regarded as an industrial by-product.

Two other preparations also made on a pilot-plant scale at the Station in Halifax from by-products of commercial cod and haddock processing were a visceral meal and a liver meal.

The visceral meal (Freeman and Hoogland, 1956) was prepared from the gastro-intestinal tracts of the fish. The sample which we tested had been drum

¹Received for publication July 22, 1960.

²Issued as N.R.C. No. 6119.

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dried to a moisture content of 7%. It contained 4% fat. The nitrogen content was 10.9%, 88% of which was non-protein nitrogen.

The liver meal (Power and Vandenheuvel, 1950; Guttman, 1950) was made by drying the residue from the extraction of cod liver oil. The sample which we tested had been dried to 8% moisture, and contained 12% residual fat. The nitrogen content was 8.7%, almost half of which was present in free amino acids. There was an apparent carbohydrate content of about 10%.

There is interest in the possibility of using the visceral and liver meals as animal food. In relation to this application the most important basic information to be obtained concerns the nutritional value as proteins of their nitrogenous constituents. We did the appropriate tests for this, and also used the same tests for another study of the quality of the protein of fish flour.

The amino acid composition of the visceral and liver meals has not been determined.

The nutritional quality of a protein can be deduced from its amino acid composition if it is known that the digestion of the protein and absorption of the products are complete or nearly so. Otherwise, and always for confirmatory purposes, biological tests are necessary to establish it. There are two widely used methods for obtaining expressions of the nutritional quality. Both involve the feeding of the protein in a balanced diet, for which rats are commonly used. One acquires information on increase in body weight in relation to the intake of protein, the appropriate expression of which is called the *protein efficiency ratio*. The other provides data which allow comparison of the amounts of the ingested and the excreted nitrogen, the difference between which amounts is termed the *nitrogen balance*. The amount of the absorbed nitrogen which is retained can be calculated if the nitrogen in faeces and urine is determined separately, which also allows an estimation of the degree of digestibility of the protein. An expression of the proportion of the absorbed nitrogen which is retained is called the *biological value* of the protein. It differs from the *protein efficiency ratio* by transcending the factor of digestibility. Our experiments provided data for expressing both *protein efficiency ratio* and *biological value*.

The amount of nitrogen in the urine increases with decreasing quality of the dietary protein, but the output of creatinine ordinarily remains constant. Therefore the creatinine portion of the urinary nitrogen varies directly with the quality of the protein. Murlin *et al.* (1953) established this relationship, and pointed out its usefulness in assessing the biological quality of proteins. With this purpose we also determined the urinary creatinine.

PROCEDURE

Some of the diets contained about 11, and some 9 to 10% nitrogenous material calculated as protein ($N \times 6.25$). The first were used to test the fish flour, and the others to test the visceral and liver meals. The difference was necessary because of the lower nitrogen content of the two meals. Egg albumin and casein were used as reference proteins in both cases. In both series the diets

containing the most concentrated protein sources were diluted with cellulose to assist in making those in each series essentially the same in nitrogen content and caloric value. Table I shows the composition of the diets.

TABLE I. The composition of diets.

Group: Source of nitrogen:	I Fish flour	II Egg albumin	III Casein	IV Liver meal	V Egg albumin	VI Visceral meal	VII Casein
	%	%	%	%	%	%	%
Nitrogenous constituent	11	12	12	18	10	15	10
Corn oil	10	10	10	10	10	10	10
Salt mixture ^a	4	4	4	4	4	4	4
Sucrose	73.8	73.8	74.4	71.9	71.6	71.8	71.8
Cellulose	1.1	0	0	0	2.2	0	2.6
Sum	99.9	99.8	100.4	103.9	97.8	100.8	98.4
Nitrogen	1.69	1.70	1.69	1.55	1.54	1.39	1.47
Crude protein (N × 6.25)	11	11	11	10	10	9	9

Supplements added per kilogram:

Cod liver oil concentrate ^b	2 mg (400 i.u. vitamin A and 100 i.u. vitamin D)
α -Tocopherol acetate	30 mg
2-Methyl naphthoquinone	1 mg
Choline chloride	1 g
Inositol	200 mg
Thiamine hydrochloride	2 mg
Riboflavin	3 mg
Pyridoxin hydrochloride	2 mg
Calcium pantothenate	15 mg
Nicotinic acid	2 mg
<i>p</i> -Aminobenzoic acid	1 mg
Biotin	0.3 mg
Folic acid	0.3 mg

^aWesson's (1932) modification of the Osborne and Mendel salt mixture, purchased as Salt Mixture W from Nutritional Biochemicals Corp., Cleveland, Ohio.

^bAyerst, McKenna & Harrison, Ltd. (Montreal) Special Formula No. 33101, containing 200,000 i.u. of vitamin A and 50,000 i.u. of vitamin D per gram.

Each group consisted of 10 rats, 5 of each sex. The average body weight of those used to test the fish flour (Groups I-III) was 75 g, and of the others (Groups IV-VII) 72 g.

The individual consumption of food was 8 to 12 g per day. An accurate record was kept of the amount consumed by each rat throughout the experimental period, which lasted for 14 days. Water was allowed *ad libitum*. The animals were weighed twice a week.

The rats were accommodated individually in cages with wire-mesh bottoms. On the 14th day they were kept in metabolism cages, and the faeces and urine for 24 hours were collected.

From data on the growth, food consumption, and the excretion of nitrogen, various measures of the utilization of nitrogen, including those indicating the nutritional value of the proteins and nitrogenous material, were calculated.

Nitrogen was determined in food, urine, and faeces by a titrimetric micro-Kjeldahl procedure (Hiller *et al.*, 1948; Sobel *et al.*, 1944), and creatinine by the method of Clark and Thompson (1949).

TABLE II. The utilization of nitrogen by rats.

Group, and source of nitrogen	Entire period, 14 days				Ranges, averages, and standard deviations, $N = 10$				
	Av. weight gain per day	Total weight gain	Total N ingested	Grams weight gain per gram N ingested	Intake of N	N in faeces	N in urine	Creatinine N in urine	Urinary N in creatinine
	grams	grams	grams		milligrams	milligrams	milligrams	milligrams	%
I	3.6 - 4.4	51 - 61	2.56 - 2.77	18.4 - 22.3	229 - 254	14 - 27	51 - 117	1.3 - 1.9	1.5 - 2.8
Fish flour	4.0 ± 0.25	56 ± 3.5	2.71 ± 0.06	20.5 ± 1.1	248 ± 9.9	21 ± 4.0	73 ± 18.9	1.6 ± 0.30	2.2 ± 0.4
II	3.0 - 4.5	42 - 63	2.41 - 2.77	16.4 - 23.1	219 - 255	10 - 27	37 - 74	1.4 - 2.2	2.4 - 3.9
Egg albumin	3.8 ± 0.54	53 ± 7.5	2.65 ± 0.11	20.1 ± 3.0	248 ± 13.3	20 ± 5.4	56 ± 10.4	1.7 ± 0.19	3.1 ± 0.5
III	2.4 - 3.6	34 - 51	2.44 - 2.73	13.6 - 19.1	185 - 256	10 - 24	71 - 106	1.1 - 1.7	1.3 - 1.6
Casein	3.1 ± 0.41	43 ± 5.7	2.59 ± 0.09	16.6 ± 2.0	244 ± 21.6	18 ± 5.0	86 ± 10.9	1.3 ± 0.17	1.5 ± 0.1
IV	0.4 - 1.1	6 - 16	1.78 - 2.09	3.4 - 7.8	109 - 176	17 - 31	42 - 63	1.0 - 1.8	2.3 - 3.5
Liver meal	0.8 ± 0.19	11 ± 2.6	1.96 ± 0.11	5.6 ± 1.2	150 ± 24.5	25 ± 5.0	52 ± 6.6	1.4 ± 0.25	2.7 ± 0.5
V	3.0 - 3.9	42 - 55	2.29 - 2.73	16.1 - 24.0	176 - 231	7 - 33	41 - 79	1.1 - 1.9	2.2 - 3.7
Egg albumin	3.4 ± 0.31	48 ± 4.4	2.55 ± 0.12	18.8 ± 2.2	220 ± 20.7	18 ± 7.3	56 ± 8.6	1.6 ± 0.26	2.9 ± 0.5
VI	(-0.3) - 0.7	(-4) - 10	1.44 - 1.81	0 - 6.4	99 - 177	7 - 15	38 - 63	1.0 - 1.6	2.0 - 3.4
Visceral meal	0.2 ± 0.36	3 ± 5.1	1.57 ± 0.11	2.3 ± 2.9	138 ± 28.9	12 ± 2.8	47 ± 9.4	1.3 ± 0.18	2.8 ± 0.5
VII	1.5 - 3.4	21 - 47	2.01 - 2.55	10.4 - 18.8	104 - 221	12 - 37	49 - 73	0.7 - 1.3	1.2 - 2.0
Casein	2.5 ± 0.50	35 ± 7.0	2.36 ± 0.21	14.5 ± 2.4	206 ± 38.9	21 ± 7.8	65 ± 7.4	1.0 ± 0.19	1.6 ± 0.2

* (ingested N) - (faecal + urinary N)

Proportion of absorbed N retained	N*	Proportion of ingested N absorbed	Proportion of absorbed N retained
	balance	%	%
I	143 - 166	89 - 94	50 - 75
Fish flour	153 ± 14.1	92 ± 1.8	68 ± 7.3
II	147 - 185	89 - 95	67 - 82
Egg albumin	172 ± 12.0	92 ± 2.1	75 ± 4.5
III	83 - 159	90 - 96	51 - 66
Casein	140 ± 21.8	93 ± 2.1	62 ± 5.3
IV	34 - 103	74 - 88	42 - 67
Liver meal	74 ± 21.9	83 ± 4.5	58 ± 8.0
V	112 - 164	86 - 96	63 - 77
Egg albumin	146 ± 15.7	92 ± 2.8	72 ± 4.5
VI	51 - 106	86 - 94	55 - 68
Visceral meal	79 ± 19.9	91 ± 2.3	62 ± 4.8
VII	110 - 140	83 - 95	60 - 70
Casein	130 ± 9.9	90 ± 3.8	66 ± 2.8

RESULTS AND DISCUSSION

The results are shown in Table II.

The proportion of the ingested nitrogen which is absorbed is a measure of the digestibility of a protein. The figures for this show that digestibility is high, and the same, for egg albumin, casein, and the protein of fish flour.

Morrison and Campbell (1960) obtained *protein efficiency ratios* of 3.80 and 3.04 for fish flour and casein respectively when they were fed at levels to supply 10% protein in the diets. If our figures for Groups I–III are expressed in the same way, *i.e.* as grams weight gain per gram protein ingested, they are 3.3, 3.2, and 2.7 for fish flour, egg albumin, and casein respectively. The ratio of the value for fish flour to casein is 1.25 in their test and 1.22 in ours, which denotes agreement. Our figures also show that for this measure of quality fish flour is the same as egg albumin, which is a high-quality protein and often used as a standard in testing.

The figures for nitrogen balance and the proportion of the absorbed nitrogen retained indicate that the protein of fish flour is intermediate between egg albumin and casein. In both cases the average figure for the fish protein is 90% of that for egg albumin and 110% of that for casein. In the case of the proportion of the urinary nitrogen in creatinine, corresponding figures are 70% and 150%.

The *essential amino acid index* (Oser, 1959a) of a protein or a food which contains protein is in many cases proportional to its *biological value* (Oser, 1959b). When these indices are calculated from the amino acid composition of fish flour (Guttmann and Vandenheuvel, 1957) and of egg albumin (Block and Bolling, 1951) they are 92 and 102 respectively, and are therefore in accord with the *biological values*.

The quality as protein of the visceral and liver meals was very different from that of the muscle preparation.

The appropriate figures in Table II indicate that the nitrogenous constituents of the visceral meal were highly digestible, and the same as egg albumin and casein in this regard. The digestibility of the liver meal, however, was considerably poorer.

Growth was negligible when the visceral meal supplied the nitrogen. The liver meal was better in this respect, despite its poorer digestibility, but nevertheless growth was very poor. The difference between these two preparations in their ability to support growth is shown in their *protein efficiency ratios*, which are both far lower than those of egg albumin and casein. In *biological value* they are essentially the same, and in this measure of quality they do not differ so greatly from egg albumin and casein.

The figures for the percentage of the urinary nitrogen in creatinine are consistent with the *biological values* of fish flour, egg albumin, and casein, but they are not in the case of the liver and visceral preparations. This index cannot therefore be used as a measure of the protein quality of these preparations.

The information which we have obtained does not necessarily define the value of the liver and visceral meals under conditions where they might be used

in animal diets in conjunction with other sources of protein or nitrogen. These data indicate that their nitrogenous constituents are in themselves of poor quality as protein or protein substitutes, and as sole sources of nitrogen will not adequately support animals with dietary requirements for certain preformed (essential) amino acids.

SUMMARY

Standard tests with young rats were applied to investigate the digestibility and the nutritional quality as protein of dried, defatted cod and haddock muscle (fish flour), cod and haddock visceral meal, and cod liver meal. Egg albumin and casein were used as reference proteins.

The apparent digestibility (proportion of the ingested nitrogen absorbed) of fish flour and visceral meal was high, and the same as that of egg albumin and casein. That of liver meal was about 9% lower.

The *protein efficiency ratio*, a measure of the promotion of growth by a given quantity of nitrogenous material, was the same for fish flour and egg albumin, and was 20% lower for casein. The *biological value*, a measure of the retention of the nitrogen absorbed from digestion, was for fish flour 10% lower than that for egg albumin and 10% higher than that for casein. These values establish the protein of fish flour as among the best in nutritional quality.

The *protein efficiency ratios* of casein, liver meal, and visceral meal respectively were 23, 70, and 88% lower than that for egg albumin. For the same materials in the same order, nitrogen balance [ingested nitrogen-(faecal + urinary nitrogen)] were 11, 49, and 46%, and measures of *biological value* were 8, 20, and 14% lower than those for egg albumin. Such values indicate that the liver and visceral meals are of poor quality, and unacceptable as sole sources of protein or as protein substitutes for animals with dietary requirements for certain essential amino acids.

ACKNOWLEDGMENTS

We were assisted in this work by Mr M. W. McLeod, Miss Joan Armstrong and Miss Verna Leonard of this laboratory. We wish to acknowledge their competent and careful work.

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The Liquefaction of British Columbia Herring by Ensilage, Proteolytic Enzymes and Acid Hydrolysis¹

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ABSTRACT

Nearly all the herring landed on the British Columbia coast during the past 10 years has been converted by the wet reduction process to animal feed, the bulk of which was in the dry form. While the final products of the wet reduction process have proven to be of a high nutritive value, in the dry form they have the disadvantage in the amount of handling required during transit. A liquid product would not only reduce handling costs but also it would act as a binder in otherwise dry feed rations.

Three methods have been tested to liquefy the whole herring: ensilage, high pressure steam liquefaction and proteolytic enzyme solubilization. In the ensilage process the liquefaction of the whole fish in an acid medium was achieved in 72 hours at 37°C. The liquefaction of the fish was shown to be due to proteolysis by the natural occurring enzymes present both in the viscera and in the flesh of the fish and was not caused by the action of bacteria. While up to 70% of the whole fish was solubilized by autoclaving the fish in an acid medium, the resulting free oil was high in free fatty acid content and the liquid concentrate dark in colour. Of the commercial proteolytic enzymes tested, pepsin achieved the highest maximum solubilization, followed by bromelin and Rhozyme B-6. An oil-protein emulsion stable at 100°C and to salting, however, was formed in the digest of each enzyme tested.

Liquid fish products were prepared under pilot-plant conditions for future nutritional assay.

GENERAL INTRODUCTION

APPROXIMATELY 200,000 TONS of herring were landed in British Columbia during 1958-1959 and almost all of the catch was converted to animal feed. The wet reduction process currently used in British Columbia to bring about the conversion of herring to animal feed yields oil, solubles, meal and whole meal (MacLeod, 1959). Previous studies conducted in these laboratories have been concerned with problems encountered during the conversion of fish (principally herring) stickwater to solubles (McBride *et al.*, 1959).

Herring meal is of high nutritive value and is widely used as a protein and growth factor source in animal feeds. There are certain advantages, however, to having a supplement to animal rations in a liquid rather than in a solid form. In a liquid form it can be more readily transported in bulk in tank cars than is the case with the dry product. Secondly, there are certain advantages to having such a substance as a binder in otherwise dry rations. Thirdly, it should be possible theoretically to prepare a liquid product more cheaply than a dry one since less steam would be required for its preparation. One disadvantage to a liquid product would be the transportation of the water in the final product.

Three methods have been proposed in the past to liquefy fish. In the ensilage process, first introduced in Finland in 1920, minced fish is acidified to pH 2.5 to

¹Received for publication November 9, 1960.

4.0 and allowed to stand for a period of approximately 2 weeks during which time liquefaction occurs (Petersen, 1951). This process, although referred to loosely as ensilage, is actually, as will be shown in this report, a liquefaction of fish resulting from natural enzymes present in the fish. This has been a popular product in Europe, especially the Scandinavian countries, for many years. Published reports indicate that the process is cheap and the product is of good quality (Hanson and Lovern, 1951).

True ensilage differs from this in that the breakdown is accomplished by the action of lactic acid bacteria in a process strictly comparable to the fermentation which takes place in a silo. The true ensilage procedure as applied to fish has been studied to a limited extent in France (Kreuzer, 1954). In another, patented process (Ryan and Wilson, 1952) fish and fish waste is liquefied by the application of steam under high pressure. The use of proteolytic enzymes to digest the fish has also been suggested but no report of a thorough investigation using these enzymes has been made. Freeman and Hoogland (1956) studied the acid and proteolytic ensilage of cod and haddock offal.

Our previous studies of problems associated with herring reduction have been extended to include an investigation of the preparation of liquid fish products from British Columbia herring. Previous studies by Tarr *et al.* (1953) showed that neither acid autolysates nor bacterial fermentation products prepared from whole herring promoted chick growth more effectively than did commercial herring meal. To approach the problem systematically it was decided to first prepare products from British Columbia herring by the established procedures, to evaluate these products, and then to determine if necessary how such procedures could be modified or new procedures devised which would give the best liquid herring product from the standpoint of cost of production, nutritive value and physical properties.

I. ENSILAGE

MATERIALS

In order to ensure uniformity of starting material for all studies, a large sample of fresh, whole herring caught in November 1958 was stored at -20°C .

METHODS

In each study of herring, whether whole or eviscerated, were ground in a meat grinder to a crude pulp. In order to facilitate pH adjustment of the pulp, one-fifth of its volume of distilled water was added and thoroughly mixed into the homogenate. The pH in each instance was adjusted at 24-hour intervals to the zero time level until the termination of the experiment. Two procedures have been suggested for the liquefaction of herring by this procedure. In one, the pH is adjusted to 2.0 with a strong acid such as HCl or H_2SO_4 . In the other, the pH is adjusted to and maintained at 4.5 with formic acid (Hanson and Lovern, 1951). Both procedures were investigated here. As a crude measurement of solubilization pH and viscosity values were determined over a 20-day period. At the completion of each experiment the product was filtered through

two layers of cheesecloth and the solids removed by filtration were then dried and weighed. After the filtrate had settled overnight in a separatory funnel, the top layer of oil was removed and discarded. The sample was then concentrated in a vacuum flash evaporator, the distillate being trapped in a flask placed in a dry-ice-acetone bath. In order to minimize the effect of heat on the final product the temperature of the water bath was kept within the range 25 to 30°C. Suitable aliquots of the concentrate were taken for viscosity determinations. Stormer viscosity determinations were carried out following a 30-minute standing period at 25°C (Rigg and Carpenter, 1912) while the pour residue test, expressed as percentage retained was determined after a setting-up period of 24 hours at 10°C (McBride *et al.*, 1959).

RESULTS AND DISCUSSION

It is evident from an examination of the rate of digestion of Samples 1A and 1B, listed in Table I, that the solids breakdown is at least initially greater when the sample is held at pH 2.0 than at pH 4.5. At the end of the twentieth day, however, the viscosity levels of the two samples are about equal. In order to test the effect of a higher temperature on the rate of solids breakdown, a second experiment was carried out at the same pH levels used in the first experiment at a temperature of 37°C. In this study, Sample 2B displayed a greater initial rate of protein breakdown at pH 2.0 than did Sample 2A at pH 4.5. Both samples, however, showed considerable solids destruction at the end of the first 24 hours of incubation. Again, by the twentieth day of digestion, only slight if any differences existed in the viscosity of the two samples.

Samples 3A and 3B listed in Table I illustrate that the ensilage of herring is due to the natural enzymes of the herring. When as in Sample 3B the herring homogenate is first heated to 95°C for 15 minutes to destroy any naturally

TABLE I. Effect of temperature and pH on the rate of solids breakdown in the production of whole and eviscerated herring ensilage.

Sample No.	Ensilage Treatment	Stormer values during ensilage ^a Time (days)								
		0	1	2	3	4	5	10	15	20
1A	Whole herring, pH 4.5, 25°C	*	*	*	29.6	17.8	17.1	15.5	14.8	14.1
1B	Whole herring, pH 2.0, 25°C	*	32.8	16.5	15.5	15.4	14.2	14.0	13.1	13.1
2A	Whole herring, pH 4.5, 37°C	*	21.2	16.8	15.1	14.8	14.2	13.4	13.3	13.3
2B	Whole herring, pH 2.0, 37°C	*	15.1	13.1	13.1	13.0	13.1	13.1	13.1	13.1
3A	Whole herring, pH 4.5 room temperature (21°C)	*	99.0	28.6	24.5	21.1	20.0	17.0	16.5	15.1
3B	Whole herring heated to 95°C for 15 min before incubation conditions same as 3A	*	*	*	*	*	*	*	*	*
4A	Whole herring, pH 4.5, 25°C	*	*	*	76.1	32.1	21.1	15.5	15.0	14.0
4B	Eviscerated herring, pH 4.5, 25°C	*	*	*	*	46.4	27.7	17.2	16.1	15.5

^aSec/100 revolutions at 25°C.

*In excess of 150 seconds.

occurring enzymes, there is little or no change in the viscosity of the resulting product on incubation. On the other hand in Sample 3A, where no heat was applied, there is a continual breakdown of the protein during the course of the incubation.

In order to ascertain whether the protein digestion was due solely to visceral enzymes or whether flesh enzymes also took part in the solids breakdown, an experiment was conducted in which the rate of breakdown of whole herring was compared with that of herring of the same batch from which the viscera had been removed. The results, Samples 4A and 4B, Table I, show that although the whole herring liquefied faster than the eviscerated ones, there was surprisingly little difference between the two samples. Much proteolytic enzyme activity must thus reside in the flesh (Siebert, 1958; Asakawa and Suda, 1957). Although the liquefaction of fish was proceeding at such a low pH that it was unlikely bacterial action could have contributed significantly to the process involved, in view of the name attached to the process and of the possibility of confusing the digestion with a true ensilage fermentation, bacterial counts were made on the digestion mixture at the beginning of a digestion at pH 2, during the course of the digestion and at the end. The system was discovered to be essentially free of bacteria on each test. It has thus been established that under the conditions used, bacteria play no part in the liquefaction process. There were no moulds visible.

The products obtained following digestion contain undigested solids and have a relatively high water content (70 to 80%). Both are undesirable from a commercial standpoint. In an attempt to overcome these disadvantages the products following complete digestion were filtered and then concentrated to a level of 45 to 50% total solids.

The proximate analysis and viscosity values of the concentrates along with the dry weight of the solids removed by filtration are shown in Table II. The amount of solids removed by filtration of the ensilage digest, except for Sample 4B, were all within the range of 15 to 25 g. In the case of Sample 4B, where

TABLE II. Viscosities and proximate analysis of herring ensilage concentrates.

Sample No.	Stormer*	Filtered solids (dry weight)	Total solids	Retained	Protein	Oil
		grams	grams	%	%	%
1A	16.5	19.82	45.1	100.00	27.5	10.20
1B	16.5	15.31	45.2	2.8	29.4	4.74
2A	17.7	25.61	48.0	5.3	33.4	3.68
2B	19.2	20.88	50.6	11.5	31.0	5.84
3A	17.3	21.16	44.4	100.00	26.2	9.05
3B ^b	—	—	—	—	—	—
4A	48.8	20.05	44.6	98.3	30.0	6.55
4B	35.1	54.14	43.9	91.7	25.0	15.80

*Sec/100 revolutions at 25°C.

^bSample not concentrated.

eviscerated herring was used, considerably more undigested solids were removed by filtering.

Although all the concentrates listed in Table II except Samples 4A and 4B indicated satisfactory Stormer values of under 30 seconds, only Samples 1B, 2A and 2B gave good pour residue tests. The high percentage retentions found in Samples 1A, 3A, 4A and 4B can be explained in part by the high oil contents in these samples. Herring oil, present as a protein-oil emulsion in these samples, solidifies at 10°C, the temperature used for pour residue determinations.

Although the initial results obtained to date would suggest that this procedure has many possible merits it has, however, one obvious demerit from a commercial viewpoint. The length of time required to obtain sufficient digestion would make it necessary to have a considerable number of large-capacity digestion tanks for an operation of any considerable size.

II. PROTEOLYTIC ENZYMES

In the previous section the use of naturally occurring proteolytic enzymes of the herring has been shown to give rise to a product which has some very desirable characteristics. Unfortunately, however, the process is slow. The most obvious way of increasing the rate of digestion is to add more enzymes. This has been considered and tested in the past by others but no report of any detailed study has been published.

The initial phases of this study were focussed on determining the capacity of several commercially available proteolytic enzymes to reduce whole herring with maximum solids breakdown to a suitable liquid product.

PRE-HEATED HOMOGENATES

Since it is generally accepted that proteolytic enzymes other than collagenases do not attack collagen but do attack gelatin, and since collagen is converted to gelatin by heat, it was of interest to determine the relative effect of the proteolytic enzymes used in these studies on heated and unheated herring.

PROCEDURE

A 500-g sample of whole herring homogenate was used in each instance. To this was added 225 ml of distilled water to facilitate pH adjustment. The enzymic level selected was 0.5% of the wet weight of the undiluted herring homogenate, and the digestion time was held to 180 minutes. In all instances the substrate was agitated continuously by stirring and the pH maintained at the desired optimum level during digestion. The pH level and temperature of digestion selected for each enzyme were the optimum levels indicated by the manufacturer of the enzyme under investigation. When the substrate was preheated this was carried out at 95°C for 10 minutes. The course of enzyme digestion was followed by noting the amount of acid required to maintain the pH constant. Following the completion of enzyme digestion each substrate was

heated in a boiling water bath for 15 minutes to insure enzyme deactivation. Upon cooling the substrate was filtered through two layers of cheesecloth. The solids removed by filtration were dried and weighed. The filtrate was then allowed to settle overnight and the top oil layer removed. Again, in order to minimize the effect of heat on the final product, the filtrate was concentrated in a flash evaporator under vacuum. The distillate was collected in a flask placed in an acetone-dry-ice bath while the temperature of the water bath was kept within the range of 25 to 30°C.

RESULTS AND DISCUSSION

The course of digestion as indicated by the amount of acid required to maintain the pH constant during digestion of both heated and unheated herring is shown in Fig. 1, using pepsin as the test enzyme. It is evident that for this enzyme proteolysis was both more rapid and more complete when preheated herring was used as the substrate. With the precooked substrate, digestion was essentially complete in 90 minutes, while with the unheated fish, levelling off of digestion occurred only after 170 to 180 minutes of incubation. The other

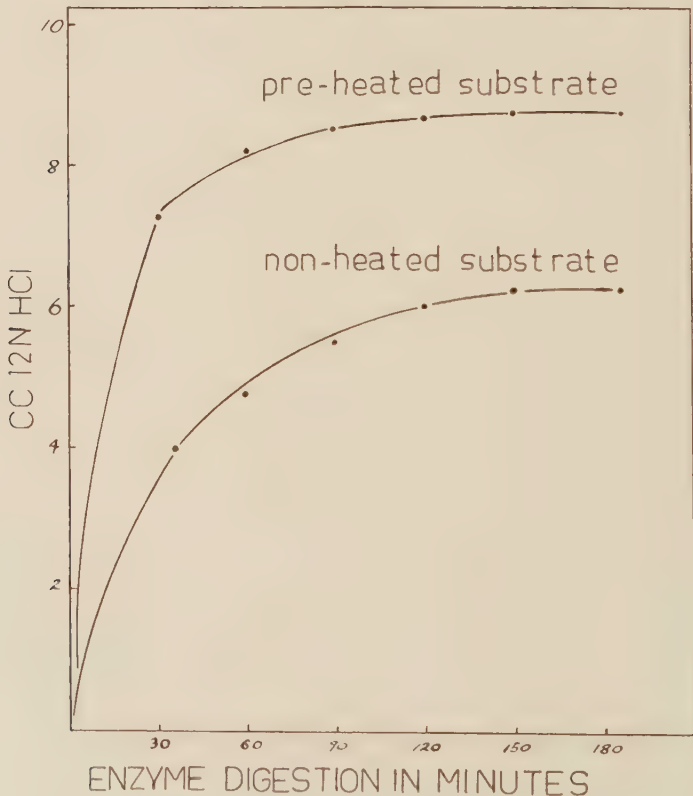


FIG. 1. Rate of pepsin proteolysis in pre-cooked and non-cooked herring homogenate.

enzymes tested, Rhozyme B-6 and protease, gave similar pH titration curves and digestion appeared to be complete in similar lengths of time. When the products from the different enzymes were examined further and concentrated, however, differences in the effects of the enzymes were apparent. The amounts of undigested material recovered from each treatment are recorded in column 4 of Table III. When the digests from the unheated fish were filtered the Rhozyme

TABLE III. Effect of several commercial proteolytic enzymes in the reduction of pre-heated and not-pre-heated whole herring to liquid fish.

Sample No.	Enzyme ^a	Substrate treatment	Protein in filtered solids
			<i>grams</i>
1A	Protease	Pre-heated	2.97
1B	Protease	Not heated	3.07
2A	Rhozyme B-6	Pre-heated	17.2
2B	Rhozyme B-6	Not heated	22.2
3A	Pepsin	Pre-heated	1.67
3B	Pepsin	Not heated	3.87

^aEnzyme digestion at the following pH and temperature: Protease pH 8.0, 50°C; Rhozyme B-6 pH 6.0, 60°C; pepsin pH 2.0, 37°C.

B-6 digest showed the greatest, and pepsin the least, amount of undigested protein. Precooking increased the amount of protein digestion in all cases.

ENZYMIC SOLUBILIZATION OF PREHEATED SUBSTRATES

INTRODUCTION

When the amount of acid or alkali required to maintain the pH constant during enzyme digestion is used to measure the extent of proteolysis, very rapid changes are observed to occur in the first 2-hour period, after which time the activity levels off. At this levelling-off point, however, solubilization of the substrate is by no means complete. The following experiment was designed to determine the degree and rate of solubilization that could be achieved.

PROCEDURE

For each experiment the substrate consisted of 1000 g of whole herring homogenate, the proximate analysis of which had been pre-determined. To this was added 500 ml of distilled water to facilitate pH adjustment. In each study the substrate was denatured prior to enzyme digestion by heating the diluted homogenate in a water bath to 85°C for 15 minutes. The enzyme level selected was 0.5% of the wet weight of the undiluted herring homogenate. In all instances the substrate was agitated continually by stirring and the pH maintained at the desired optimum level during digestion. The pH level and temperature of digestion selected for each enzyme were the optimum levels indicated by the

manufacturer for the enzyme under investigation. The digestion was allowed in each case to continue until no further increase in the percentage solubilization of the substrate was evident. Solubilization of the substrate was determined as follows: A 60-ml aliquot was taken, 10 ml being used to determine the total solids content of the whole substrate, while the remaining 50 ml was centrifuged at $20,000 \times g$ for 20 minutes. Following centrifugation, the oil which had collected at the surface was removed and the total solids content of the clear supernatant water-soluble fraction was determined. This value, coupled with that for solids minus the oil of the uncentrifuged sample, was then used to determine the percentage solubilization achieved by the enzyme.

At the completion of each enzyme digestion the substrate was centrifuged at $20,000 \times g$, the insoluble solids were collected, dried at 80°C in a vacuum oven and weighed. Also, a suitable aliquot of the oil that had been freed at the surface was taken for free fatty acid determinations. The free fatty acids were determined by the method outlined in the Official Methods of the American Oil Chemists Society and expressed as oleic acid.

RESULTS AND DISCUSSION

The data in Table IV show that pepsin gave rise to the highest percentage solubilization while Rhozyme B-6 and bromelin were about equally active. While both pepsin and bromelin achieved maximum solubilization at the end of 48 hours

TABLE IV. The effect of several commercial proteolytic enzymes on the reduction of whole herring to liquid fish.

Enzyme	Proximate analysis of the original whole herring			Enzyme digestion conditions			Insoluble solids (dry weight)	Maximum solubi- lization	Free oil	Free fatty acids in free oil
	Protein (N $\times$ 6.25)	Oil	Water	pH	Temp	Time ^d				
	%	%	%		$^{\circ}\text{C}$	hours	grams	%	%	%
Pepsin	16.40	13.16	67.10	2.0	37	48	56.14	77.8	15.0	10.80
Bromelin	16.38	13.14	67.18	4.5	60	48	88.47	64.6	18.0	7.6
Rhozyme B-6	16.44	13.20	67.05	6.0	60	72	92.34	65.5	12.0	9.7 ^e

^dTime required for maximum solubilization or point experiment terminated.

^eFree fatty acid level following 48-hr digestion 7.2%.

of digestion, Rhozyme B-6 required an additional 24-hour digestion period to reach its highest level of solubilization. The results for pancreatin and protease digestion were not included in Table IV as both were unsatisfactory due to the fact that a thick oil-protein emulsion formed when these enzymes were used. The digestion conditions for the latter two enzymes were as follows: pancreatin, pH 7.8, 37°C ; protease, pH 8.0, 40°C . The pancreatin digestion lasted for 91 hours while the protease digestion was terminated at the end of 48 hours. It is of interest that both these enzymes had optimum pH levels on the alkaline side of neutrality while the remaining enzymes tested had optimum pH levels on the acid side. Whether this difference in the optimum pH level had any effect on the formation of the emulsion is not known. Nevertheless, as the pH optimum of the enzyme

went down, the ability of the enzyme to solubilize the herring increased. The oil-protein emulsion formed was found to be present in all the enzyme-digested samples but to a much smaller extent in those where the enzyme used had an optimum pH below neutrality, in which cases the emulsion accounted for only 15 to 20% of the total volume of the digest prepared. The emulsion formed a layer immediately below the free oil, solidified at temperatures below 10°C and could be easily separated mechanically without contaminating the clear fraction below. Analysis of two of these emulsions on a wet-weight basis, one taken from a completed bromelin digest and the other from a completed pepsin digest, showed them to have a protein level of from 15.2 to 15.8% and an oil level of 30.8 to 31.1%.

The results given in Table I also show that the lowest quantity of insoluble solids was obtained from the pepsin digest and the highest amount from the Rhozyme B-6 digest with the bromelin digest giving a yield somewhat less than that obtained from the Rhozyme B-6 sample. These values agree with the results expected on the basis of the percentage solubilization obtained with the respective enzymes. The proximate analysis of the raw herring homogenates showed no apparent differences. This can be attributed to the fact, as previously mentioned, that the herring used in this investigation were all taken from a single November 1958 catch.

The free fatty acid levels of the free oil obtained at the completion of 48 hours of enzyme digestion varied inversely with the digestion pH.

OIL-PROTEIN EMULSION

As previously noted, the main difficulty encountered following the completion of the enzyme digestion is the removal of oil prior to the concentration of the digest to the finished product. On centrifuging, only a small fraction of the oil separates as free oil; the rest appears in the form of an oil-protein emulsion. If the oil in the oil-protein emulsion is allowed to remain in the final product, the product is very viscous at low temperatures. Furthermore, if the oil content of the finished product exceeds 5% on a wet-weight basis, the product would normally be considered unacceptable as a feed supplement.

As mentioned earlier, while it is possible to remove the oil emulsion mechanically by chilling the product and scraping off the solidified emulsion, this process in a commercial operation might be both cumbersome and uneconomical.

In order to study this emulsion problem further, a large pool of bromelin-solubilized liquid digest, which had not been centrifuged, and hence from which the free oil had not been removed, was prepared as outlined in Table IV. This product was divided into three equal parts and one of each of the parts was diluted with distilled water to a total solids content as follows: Part A, 18%; Part B, 12%; Part C, 6%. Using 100-ml graduates and 50-ml aliquots of the diluted digests, each test solution was subjected to a series of treatments in an attempt

to obtain maximum recovery of free oil. The procedures followed and the results obtained are given in Table V. The volumes of oil were determined after the test solutions had stood at room temperature for 24 hours following completion of the treatment.

TABLE V. Effect of autoclaving, heating to 95°C and salting on the release of free oil in solubilized liquid fish solutions of varying total solids content.

Treatment	Sample	Total solids	Total oil present	Free oil following treatment	Free oil
		%	ml	ml	%
1. Autoclaved for 30 min at 15 lb/sq in	A	18	9	7	77.7
	B	12	6	4	66.6
	C	6	3	2	66.6
2. Heated to 95°C for 30 min	A	18	9	1	11.1
	B	12	6	1	16.6
	C	6	3	0.5	16.6
3. (i) 10 mg KH_2PO_4 added (ii) Heated to 95°C for 10 min	A	18	9	2	22.2
	B	12	6	4	66.6
	C	6	3	2	66.6
4. As in No. 3 except 50 mg KH_2PO_4 added	A	18	9	3	33.3
	B	12	6	3	50.0
	C	6	3	2	66.6
5. As in No. 4 except heated to 95°C for 30 min	A	18	9	1	11.1
	B	12	6	4	66.6
	C	6	3	2	66.6

Up to 77.7% of the total oil was released as free oil upon autoclaving for 30 minutes while only 66% of the total oil existed as free oil following 30 minutes of boiling even after the addition of KH_2PO_4 . While diluting, the digest appeared to have little effect in promoting the release of oil in the autoclave treatment; the more dilute preparations yielded a higher percentage of oil in the other four treatments. From these results it is evident that the emulsion present after enzyme digestion is a very stable one and methods other than heat or salting out will have to be found to break it satisfactorily. It was reasoned, however, that by removing the greater portion of the total oil from the herring by a pre-press as is done in the present commercial reduction process, the emulsion problem might be successfully eliminated. To test this possibility an experiment was carried out where the denatured herring homogenate was pre-pressed prior to enzyme digestion. The diluted denatured herring homogenate was placed in a double-layer No. 12 canvas bag and pressed at 5,000 lb/sq inch. The press juice released was collected, transferred to a separatory funnel and allowed to stand overnight at room temperature. The free oil which separated was removed, the volume measured and the free fatty acid concentration determined. The water layer of the press liquid was added back with thorough mixing to the press pulp. The reconstituted mixture minus the free oil was digested with pepsin for 48 hours. After digestion the mixture was centrifuged, and the degree of

solubilization, the amount of free oil, its fatty acid content and the amount of emulsion present was determined. A record of the observations is given in Table VI.

TABLE VI. Effect of mechanical pressing followed by pepsin digestion on the release of free oil in a denatured herring homogenate.

Fraction	Oil recovery in the various fractions ^f
Free oil	57.5
Oil-protein emulsion	31.6
Insoluble solids	10.9
Liquid digest	0.0

^fExpressed as percentage of oil present in the original herring.

Although all the oil was not removed by pre-pressing, the amount removed (57.5%) suggests that this method does offer a possible means of at least partially by-passing the emulsion problem, particularly since under industrial conditions, where more efficient presses are employed, pressing of the cooked herring removes up to 85% of the total oil present. Furthermore, the oil obtained from the press juice was of excellent quality with a free fatty acid level of only 1.4% as compared to 7 to 10% for the free oil obtained following the enzyme solubilization of whole fish.

Upon centrifuging a suitable aliquant of the 48-hour pepsin digest of the pressed fish, it was noted that none of the remaining oil in the substrate was present as free oil. The remainder of the oil was found to be bound almost completely in the oil-protein emulsion, which accounted for approximately 10% of the total digest volume. This emulsion which on a wet-weight basis had an oil level of 30.1% contained 31.6% of the total oil present in the original herring homogenate. By calculation, the insoluble solids which would contain the remainder of the total oil in the fish held 10.9% of the oil present in the herring homogenate.

The 73.9% solubilization obtained at the end of 48 hours pepsin digestion compared favourably with previous results for non-pre-pressed substrates.

INSOLUBLE SOLIDS

It has been found that 20 to 30% of the original fish fails to be solubilized on enzyme treatment (Table VII). The insoluble solids from a pepsin digest were hydrolysed in a sealed combustion tube with 6*N* HCl. Analysis for free α -amino nitrogen revealed that after hydrolysis 69% of the total nitrogen was α -amino nitrogen, indicating that most of the nitrogen in the sample was present as protein nitrogen. It seemed not unlikely that failure to get more complete solubilization of the protein would be due to inhibition of the action of the digestive enzyme by accumulation of the products of hydrolysis. In order to test

TABLE VII. The insoluble solids content of liquid fish prepared by maximum enzyme solubilization of whole herring homogenates.

Enzyme	Substrate (dry weight)	Insoluble solids (dry weight)	Analysis insoluble solids	
			Protein	Oil
	<i>grams</i>	<i>grams</i>	<i>%</i>	<i>%</i>
Pepsin	329	56.14	66.10	19.6
Bromelin	329	88.47	66.50	12.6
Rhozyme B-6	329	92.34	63.50	15.15

this hypothesis and to make an effort to reduce the size of the insoluble fraction still further, a series of experiments was carried out in which the insoluble solids obtained following maximum solubilization were separated from the digestion mixture and subjected to fresh enzyme attack.

In the first experiment, a 48-hour pepsin digest of herring homogenate prepared as outlined in Table I was divided into two equal parts. One part was held without further treatment to serve as the control. The second part was centrifuged at $20,000 \times g$ for 20 minutes. The insoluble solids were collected and resuspended in 100 ml of distilled water. Both the control and the resuspended solids were adjusted to pH 2.0 and placed in a water bath at 37°C . To the resuspended solids was added a slurry of fresh pepsin at a level equal to one-half the amount used in the original digestion, that is, 0.25% of the total weight of the undiluted herring homogenate. The solubilization of both samples was followed until no further change was noted. The results obtained from this study are given in Table VIII, Experiment No. 1. The second experiment was

TABLE VIII. Effect of further pepsin digestion on the insoluble solids obtained from a maximum solubilized pepsin and Rhozyme B-6 digestion of whole herring.

Experiment No.	Initial maximum enzyme solubilization			Conditions and results of further treatment on the insoluble solids				Analysis of insoluble solids obtained from second digestion	
	Enzyme used	Digestion time	Solubi- lization	Enzyme added	Digestion time	Further solubi- lization ^b	Total ^a solubili- zation	Protein	Oil
		<i>hours</i>	<i>%</i>		<i>hours</i>			<i>%</i>	<i>%</i>
1. Part A (control)	Pepsin	48	77.8	—	48	0.6	78.4	66.1	19.6
Part B (test)	Pepsin	48	77.8	Pepsin	48	8.1	85.9	65.1	24.8
2. Part A (control)	Rhozyme B-6	72	67.7	—	48	7.1	74.8	69.0	16.6
Part B (test)	Rhozyme B-6	72	67.7	Pepsin	48	18.2	85.9	57.0	23.2

^aThis represents the sum of the solubilization which occurred during the initial digestion and the solubilization which resulted from further treatment of the insoluble solids.

^bExpressed as percentage of the total solids present at the beginning of the first digestion.

designed to establish whether the lower degree of solubilization achieved with Rhozyme B-6 as compared to pepsin was a pH rather than an enzyme effect. Since more bone would be solubilized at pH 2 than at pH 6, the larger amount of insoluble solids at the higher pH might merely mean a lesser dissolution of bone.

In the second experiment the insoluble solids from a Rhozyme B-6 digest were divided into two equal lots and each was suspended in a volume of distilled water equal to one-half the original digest volume. Following the adjustment of both samples to pH 2.0, the products were placed in a 37°C water bath. One sample, the control, was held without further treatment. To the other was added a slurry of pepsin at a level equal to 0.25% of the original weight of the undiluted herring homogenate. Solubilization was followed in each sample until no further change was evident. The extent of solubilization achieved is shown in Table VIII under Experiment No. 2.

Examination of the results listed in Table VIII show that the greatest additional solubilization was obtained when the insoluble solids from the Rhozyme B-6 digest were subjected to pepsin digestion. It is evident that much, but not all, of this solubilization occurred as a result of adjusting the insoluble solids suspension from pH 6 to pH 2 and hence would represent solubilization of bone. It is evident, however, that pepsin still has a somewhat greater capacity than Rhozyme B-6 to solubilize the herring, an effect which is independent of the pH of the digestion system.

The ability of fresh pepsin to further digest a suspension of insoluble solids which had been freed of components of the original reaction mixture suggests either that the reaction products inhibited further digestion or that the original pepsin had lost its activity and a supply of fresh enzyme was required to produce further solubilization.

The results obtained thus far on the rate and extent of solubilization of the whole fish clearly indicate that pepsin is the superior of the enzymes tested. On the basis of this finding the following experiments were limited to a study of pepsin.

OPTIMUM pH LEVEL FOR PEPSIN ACTIVITY

Evidence has been presented elsewhere that the optimum pH for pepsin activity on denatured bovine serum albumin and haemoglobin is 3.5 as compared to an optimum pH of 1.7 for the corresponding native substrates (Schlamowitz and Peterson, 1959). Although the results for pepsin activity presented here have all been carried out at pH 2.0, it would be highly desirable from a commercial point of view if the optimum pH level for pepsin digestion of denatured herring was 3.5. This would not only eliminate the necessity for the expensive alloy equipment required to withstand the acidity of pH 2.0, but also, if the optimum pH for pepsin activity on denatured herring was 3.5, it might shorten the length of the digestion time needed to obtain digestion at pH 2.

To test for the optimum pH for pepsin activity on a denatured herring substrate, three substrates were prepared exactly as outlined in Table IV for pepsin digestion except for the pH levels of the substrates. The pH of the first sample was adjusted to 2.0, the second sample to 3.0 and the third sample to 3.5. The level of pepsin used in each of the three samples was 0.5% of the weight of the undiluted herring homogenate and all three samples were tested simultaneously. A record was kept of the total amount of 12*N* HCl required to maintain the starting pH levels in each sample. The percentage solubilization

was determined for each sample at the end of 24 hours of digestion. The results are given in Table IX, and show clearly that the pepsin activity is significantly higher at pH 2.0 than at either pH 3.0 or 3.5.

TABLE IX. The effect of pH on the level of pepsin activity as measured by the total amount of 12*N* HCl used to maintain the desired pH and the percentage solubilization obtained following 24-hr digestion.

Sample No.	pH zero hour	Amount 12 <i>N</i> HCl used to maintain a constant pH	Solubilization following 24-hr pepsin digestion
		<i>ml</i>	%
1	2.0	26.8	63.0
2	3.0	16.2	47.1
3	3.5	8.7	38.4

OPTIMUM PEPSIN LEVEL FOR SOLUBILIZING HERRING

The use of 0.5% levels of pepsin, as with the other enzymes studied, was based on the arbitrary suggestion of the enzyme manufacturers rather than on experimental findings using herring as the substrate. To determine the optimum level of pepsin for maximum solubilization an experiment was carried out using three separate substrates, each prepared exactly as before except for the enzyme level tested. The three levels of pepsin selected were 0.1, 0.3 and 0.5%, based on the weight of the undiluted herring homogenate. Again, all three digestions were carried out simultaneously. In this study the change in the pH during

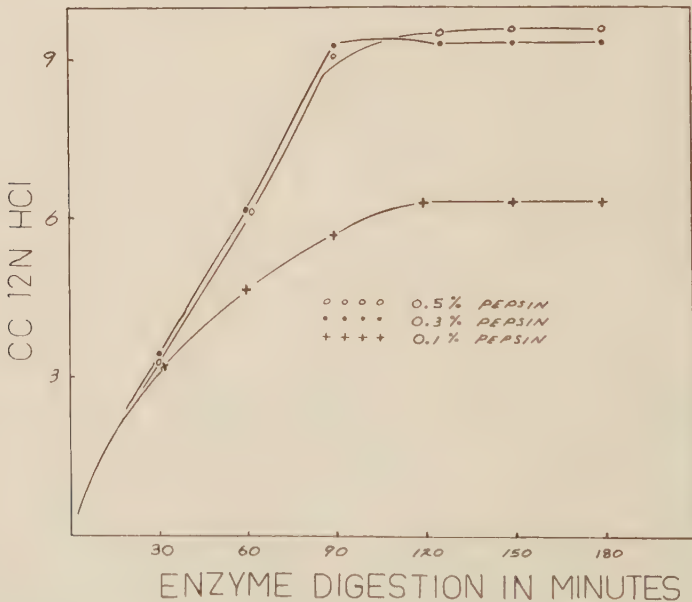


FIG. 2. Rate of pepsin proteolysis at 0.5, 0.3 and 0.1% enzyme concentrations in denatured herring homogenate.

digestion was used as an index of enzyme activity. The experiment was terminated at the end of 3.5 hours of enzyme digestion. The rate of digestion as indicated by the amount of acid required to maintain the pH constant during digestion is shown in Fig. 2.

It is evident from an examination of the curves given in Fig. 2 that following the initial 20 minutes of incubation the pepsin proteolysis is faster at the 0.3 and 0.5% enzyme levels than at the 0.1% level. There appears to be no apparent difference in the rate of proteolysis at the 0.3 and 0.5% enzyme concentrations.

III. HIGH-TEMPERATURE ACID HYDROLYSIS

LABORATORY STUDIES

The method of using steam under high pressure to liquefy non-fatty fish scraps which have been previously acidified to a pH of 2 to 4 is used extensively on the eastern coast of this continent. Although the process has not been developed to include fatty fish such as herring, the manufacturers using this process claim good physical and chemical properties for their products. As we are not aware of any detailed report on the use of this process with fatty fish, a study of the process was carried out using herring.

The apparatus used in this study to hold the sample under the desired steam pressure consisted of a large monel-alloy cylindrical tank fitted with a removable top. A large stirrer which could be removed when not in use was available for mixing large batches of fish. A closed inside circular steam line was connected to an external steam generator which furnished the required steam pressure at a constant level for the period of the experiment.

In order to test both the operation of the apparatus and the efficiency of the process, a 600-g batch of whole herring homogenate was diluted with 120 ml of distilled water and then adjusted to pH 1.0 with concentrated H_2SO_4 . The acidified product, held in a 1-litre beaker, was covered with a large petrie dish and the beaker plus contents suspended by wire in the steam tank. The tank was sealed, brought to a steam pressure of 50 lb/sq in (300°C) for 3 hours and then cooled. The tests used and the results obtained when the cooled product was analyzed were as follows: solubilization, 69.9%; free oil in the total oil, 66.4%; free fatty acids in the free oil, 7.5%. The most significant difference between this product and that prepared by proteolytic enzymes was the complete absence of any oil protein emulsion in the pressure cooked sample. While the percentage solubilization achieved in this steam-cooked sample was somewhat lower than that achieved in the maximum solubilized pepsin sample, it is, however, higher than that achieved in the maximum solubilized bromelin and Rhozyme B-6 samples. Furthermore, the percentage of the total oil existing as free oil in the pressure sample was approximately 4.5 times as great as in the enzyme-solubilized products. The free fatty acid level of 7.5% obtained in the free oil of the pressure sample did not differ significantly from the levels obtained for the corresponding enzyme products. The steam pressure prepared liquid fish did, however, have a much darker colour than the finished enzyme sample, as well as a slightly burnt odour.

PILOT-PLANT STUDIES

This phase of the study was carried out with the collaboration of Mr F. Claggett of this Station.

Normally the pilot plant is used to test the efficiency of the finalized procedures developed in the laboratory under conditions more likely to exist in an industrial plant. This, however, was not possible in the present investigation due not only to the volume limitations of the pilot plant itself but also to the physical nature of the product being handled. As only a few pounds of finished product can be prepared at any one time, the pilot plant is run on a batch basis rather than as a continuous process. In such an operation considerable amounts of the product are lost through numerous transfers in the plant during heating, cooling and centrifuging of the dilute sample. As the finished product is fairly viscous, further losses due to the sticking of the product to the sides of the evaporator and the outlet pipes are incurred during removal of the finished product. These losses make it impossible to obtain accurate quantitative data on the operating efficiency of the plant. The pilot plant was used, however, to prepare pepsin-solubilized liquid fish and pressurized liquid fish in sufficient quantities to be tested at a later date in conjunction with commercial herring solubles, commercial meal and commercial whole meal for their respective nutritive values as a supplement in chicken feed rations.

MATERIALS

The herring used for the production of all five of the products just mentioned was taken from a single commercial "set" in November 1959. The herring selected for enzyme and steam-pressure solubilization were stored in 4-gallon (18-litre) liver cans at 10°F until required for processing. Since the required volume of liquid fish concentrate prepared by each of the two processes greatly exceeded the processing capacities of the pilot-plant equipment, the whole herring were divided roughly into 50-lb batches and processed on a batch basis.

METHODS

For pepsin solubilization the procedure used was as follows: The herring were homogenized with the use of an electrical cutter and then diluted with one-half their weight of distilled water. Denaturation of the sample was accomplished by heating the diluted herring homogenate to 90°C for 20 minutes. To avoid scorching, the homogenate was stirred continuously during heating. Upon cooling, the temperature and pH of the homogenate was adjusted to the optimum for pepsin digestion, that is, to 37°C and pH 2.0. Following the addition to the homogenate of a slurry of pepsin in water at a level equal to 0.5% of the undiluted herring homogenate, digestion was allowed to proceed for a period of 48 hours. At the completion of each enzyme digestion period the substrate was adjusted to pH 4.0 to prevent corrosion of pilot-plant equipment and heated to 99°C to ensure maximum oil separation. The heated substrate was centri-

fuged through a Centriwesta centrifuge twice, first with the chamber bowl to remove insoluble solids and then with the disc bowl to separate the free oil. Both the oil and the insoluble solids removed by centrifuging were collected separately. The insoluble solids were dried at 80°C in a vacuum oven and weighed. The clarified liquid fish was then stored in wide-mouth 4-gallon liver cans at 0°C overnight to facilitate settling and solidification of the oil emulsion. After oil emulsion removal by scraping off the solidified layer, the solubilized liquid sample was concentrated *in vacuo* in a pilot-plant concentrator.

For the preparation of steam-pressurized liquid fish the herring homogenate was diluted as outlined for the enzyme sample with distilled water, adjusted to pH 1.0 with concentrated H₂SO₄ and pressure cooked at 50 lb/sq inch (300°C) for 3 hours with continuous stirring. When cool it was adjusted to pH 4.0 and the oil and insoluble solids were removed by centrifuging as outlined for the pepsin digest. The clarified sample was then concentrated *in vacuo* in the pilot plant.

Each of the products was analyzed for oil, water, ash, protein and total solids. Viscosity tests were carried out on the liquid products.

RESULTS AND DISCUSSION

When the data from the two liquid fish products listed in Table X are compared on a 100% total solids basis to the corresponding results obtained for

TABLE X. Analysis and viscosity tests of a pressure and a pepsin solubilized liquid fish concentrate and comparison of the analyses with that of commercial meal and whole meal.

Analysis (wet weight)	Acid-pressure liquid fish (Station product)		Pepsin-solubilized liquid fish (Station product)		Meal (commercial)		Meal (commercial) (whole)	
	Actual% total solids ¹	100% total solids ¹	Actual% total solids	100% total solids	Actual% total solids	100% total solids	Actual% total solids	100% total solids
Water (%)	57.00	0.00	65.0	0.00	7.70	0.0	7.90	0.00
Total solids (%)	43.00	100.00	35.0	100.00	92.30	100.0	92.10	100.00
Protein (%)	32.90	76.60	22.10	63.10	74.00	80.10	74.50	81.00
Oil (%)	1.91	4.45	5.60	16.00	8.94	9.69	9.42	10.20
Ash (%)	8.22	19.10	6.80	19.40	9.10	9.85	8.32	9.05
Viscosity test								
Stormer ²	17.90	—	16.4	—	—	—	—	—

¹Analyses are given both for the actual solids content of the product as well as for a product calculated to contain 100% solids for ease of comparison with the results for meal.

²Seconds/100 revolutions/200 g weight. Test after sample held for 2 hours at 25°C.

the meal and whole meal products, it is evident that the protein content of the two meal samples is somewhat higher than found in the two liquid products. On the other hand, the ash values of the two liquid fish products were approximately equal and about double the ash levels found in the two meal products. While the oil levels of the two meal samples were about equal, the oil content of the pressure-solubilized liquid fish sample was about one-half that found in the two meals and

approximately one-quarter that present in the enzyme-solubilized liquid fish concentrate. These four products, although similar in that each contains the greater portion of the original constituents of the raw herring, do however have some significant differences in their preparation. Meal is that part of the herring obtained in the reduction process following the removal of the press juice. The press juice is kept separate and utilized following the removal of free oil, in the production of herring solubles. Whole meal on the other hand is meal to which has been added a portion of the herring solubles. The amount of solubles added to the meal for the production of the whole meal varies from 10 to 40% depending upon operating conditions and economic demand for solubles as a separate product at the time. As the pre-pressing of herring results in a press juice containing substantial amounts of the total oil and ash present in the raw herring, one would expect the meal sample to contain smaller amounts of these two constituents than would the whole meal. In actual fact the oil content of the meal sample was somewhat lower than noted in the whole meal sample. The ash level of the meal product, however, was slightly higher than the whole meal product.

As a complete removal of the oil-protein emulsion was not accomplished in the liquid enzyme preparation due to mechanical difficulties encountered in working with large volumes of dilute digest, the oil level of this product is significantly greater than that obtained in the other finished products. It is evident from an examination of the proximate analysis of this product that the oil is displacing the protein and not the ash.

Thus, the results obtained for these four products indicate that if each sample is prepared under optimum operating conditions, each product on a 100% total solids basis would have approximately the same protein content. Furthermore, while the ash level in the two liquid fish products would be about double that amount present in the two meal samples, the oil content of the two meal samples would be about double that present in the two liquid fish products.

COMPARISON AMONG PROCESSES

As previously noted, it is not possible to calculate the efficiency of the two liquefaction processes on the basis of the results obtained from the pilot plant operation. It is possible, however, to obtain some idea of their efficiency from the results obtained in the small-scale studies carried out in the laboratory. In Table I are listed the amounts of commercial solubles, commercial meal, commercial whole meal, pepsin-solubilized liquid fish and pressure-solubilized fish plus their respective by-products obtainable from one ton of whole raw November herring. The figures given for meal, whole meal and solubles are based on actual production data obtained from a local fishing company. The liquid fish product results obtained by both pepsin and pressure solubilization have been based on laboratory findings obtained under optimum conditions.

The data in Table XI indicate that whereas in herring reduction to meal the nitrogenous components of the original herring are found in two fractions, when herring is solubilized to a liquid fish product, at least by enzymes, the nitrogen appears in three. Two of these, the oil-protein emulsion and the insoluble solids,

TABLE XI. A comparison of herring reduction by three methods, enzyme solubilization, pressure solubilization and conversion to meal and solubles from the standpoint of product yield and composition.

Treatment	Products formed	Yield ^a		Components			
		Wet weight	Dry weight	Protein	Ash	Oil	Free fatty acid
		<i>pounds</i>			<i>pounds</i>		
Pepsin solubilized ¹	Liquid fish	498	249	199	50	0	—
	Free oil	—	39	—	—	28.2	10.8
	Oil-protein emulsion	450	203	68	—	135	—
	Insoluble solids	408	182	54	42	86	—
Pressure solubilized ^m	Liquid fish	446	223	179	44	0	—
	Free oil	—	207	—	—	199.5	7.5
	Oil-protein emulsion	0	0	—	—	—	—
	Insoluble solids	602	380	142	185	53	—
Reduction to whole meal (10% solubles added back)	Whole meal	—	385	293	36	38	—
	Free oil	—	202	—	—	—	1.0
Reduction to meal, oil and solubles	Meal	—	350	259	32	31	—
	Free oil	—	202	—	—	—	1.0
	Solubles	150	75	53	15	7.5	—

^aCalculations based on the reduction of 2000 lb of November-caught herring containing a total of 320 lb protein, 260 lb oil, and 52 lb ash.

¹Based on 78% solubilization.

^mBased on 70% solubilization.

would probably be unsuitable for ordinary feeding purposes. The product formed in the solubilization process which is comparable with fish meal is the liquid fish fraction itself. It is clear that in both solubilization processes the recovery of protein is considerably less in this fraction than in fish meal. Unless this liquid fish fraction can be shown to have a nutritive value which will compensate for its lower protein content, it would appear unlikely that this process would be competitive with fish meal.

In the enzyme but not the pressure liquefaction process, only a small percentage of the total oil is recoverable as free oil and the quality of this is judged by its free fatty acid content is low. As herring oil is one of the more valuable by-products of herring reduction, this poor oil recovery would be a further disadvantage of the process.

The insoluble solids which separate during oil recovery in the liquefaction processes, unless they can be resuspended in the liquid fish fraction, would represent a considerable loss of the total solids content of the original fish.

It would appear that unless the liquid fish fraction proved to be a really premium product which could demand a special price, it is unlikely that herring reduction by either liquefaction process would be competitive with a fish-meal operation.

ACKNOWLEDGMENTS

The herring for this investigation were obtained from the British Columbia Packers Imperial Plant at Steveston, B.C. The authors wish to thank the Rohm and Haas Co., Philadelphia, Pa., for samples of Rhozyme B-6; Takamine Laboratory, Inc., Clifton, N.J., for samples of bromelin and protease, and H. Reesman Corp., New York, N.Y., for samples of pepsin.

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The Protein Nutritive Value of "Liquid Herring" Preparations¹

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ABSTRACT

Experimentally prepared "liquid fish" made from British Columbia herring was compared with presscake herring meal, whole herring meal and condensed herring solubles as a source of supplementary protein for chicks. Two samples of liquid fish made by an enzymatic and by a high-pressure acid treatment respectively were tested. The two preparations were similar in protein value and gave a growth response intermediate between that obtained with herring meal and with condensed herring solubles.

INTRODUCTION

AN INCREASING AMOUNT of the herring meal produced in British Columbia contains material that was formerly either lost in the discarded presswater or, if the presswater were reclaimed, was marketed separately as condensed herring solubles. The possibility was suggested that the herring reduction process might be altered to produce oil and a liquid preparation of the entire fish. Today's feed manufacturing plants are designed to handle the addition of liquids or semi-liquids, e.g. molasses, feeding oil, tallow, or condensed fish solubles, to mixed rations. Accordingly it was felt that if a "liquid fish" could be successfully prepared it might find wide acceptance provided it could be shown to be of high nutritive value.

MATERIALS AND METHODS

Two preparations of liquid fish were made by an enzymatic and high-pressure acid process respectively (McBride, Idler and MacLeod, 1961). The nutritive value of the liquid fish was compared with that of commercial British

¹Received for publication November 9, 1960.

Columbia samples of condensed herring solubles, presscake herring meal and whole (i.e. presscake plus solubles) herring meal in chick tests. The chemical compositions of the materials tested are given in Table I.

TABLE I. Proximate analysis of various herring supplements used in the chick rations.

Supplement	Solids	Protein	Oil	Ash	pH
	%	%	%	%	
Enzyme-treated liquid fish	35.0	22.1	5.6	6.8	4.00
Pressure (acid)-cooked liquid fish	43.0	32.9	1.9	8.2	4.82
Commercial condensed herring solubles	47.2	35.2	3.9	8.4	4.10
Presscake herring meal	92.3	74.0	8.9	9.1	—
Whole herring meal	92.1	74.5	9.4	8.3	—

The formula of the basal diet with which the different products were fed was as follows: dextrose 16.0, ground yellow corn 76.0, dehydrated cereal grass 2.5, distillers dried solubles 2.0, iodized salt 0.5, bonemeal 2.0, limestone 1.0, and manganese sulphate 0.014 lb per 100 lb; vitamin A 2000 I.U. and vitamin D₃ 120 I.C.U. per lb. This basal mixture contained 8.2% protein (% nitrogen $\times$ 6.25). Each of the products to be tested was added to supply 3% of protein in the total diet. A mixture of isolated soybean protein and amino acids in the following proportions was employed as a reference protein: isolated soybean protein (91% protein) 100, *dl*-methionine 2, glycine 3, and lysine hydrochloride 3.5.

The chicks used were White Leghorn cockerels. They were fed the basal diet without supplementary protein for 2 weeks. At 2 weeks the population was reduced by eliminating the slowest and the most rapidly growing chicks. Eighteen standardized lots of 15 chicks each were made up and each diet was fed to triplicate lots for 20 days.

RESULTS

FLUCTUATION IN THE TEMPERATURES OF THE PREPARED CHICK DIETS

The diet containing the enzyme-treated liquid fish heated considerably and reached a temperature of 43 to 44°C during the third week after mixing. Subsequently the temperature dropped. The diet containing the liquid fish prepared by acid treatment showed no evidence of fermentation until the 23rd day and had heated to 33°C at the time the experiment was completed. The highest temperature noted in the reference diet was 22°C.

CHANGES IN THE WEIGHT GAIN OF THE CHICKS

The growth responses of the chicks to the different preparations as protein supplements are shown graphically in Fig. 1. The average weights of the birds

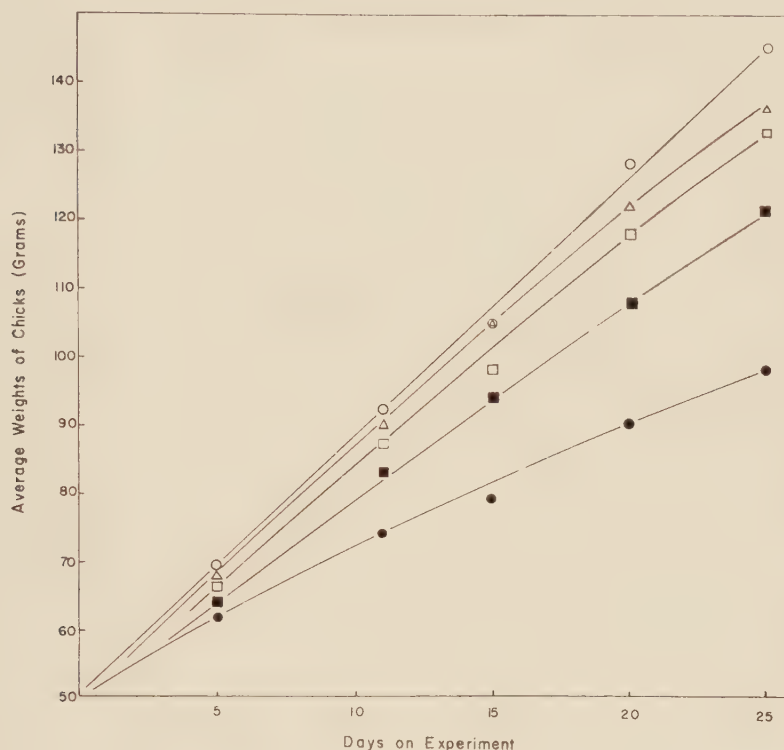


FIG. 1. Growth response of chicks to herring product supplements.
 ○ Presscake meal. △ Whole meal. □ Reference protein. ■ Liquid fish
 (acid-treated and enzyme-treated). ● Condensed solubles.

after 20 days on the experimental diets and the efficiency of feed utilization to this time are given in Table II. Mortality during the last 5 days of the experiment made calculations of the feed efficiency for this period meaningless.

TABLE II. Average weights of chicks and efficiency of feed utilization at 20 days of age.

Supplement	Average weight	Feed efficiency (feed/gain)
	<i>grams</i>	
Reference protein	118	3.74
Enzyme-treated liquid fish	108	3.76
Pressure (acid)-cooked liquid fish	108	3.73
Condensed herring solubles	90	4.72
Presscake herring meal	128	3.46
Whole herring meal	122	3.44

DISCUSSION

The ratio of gain of chicks fed the two types of liquid fish were similar and intermediate between the growth rates of the chicks fed meal and condensed solubles respectively. Unfortunately, as a result of the fermentation in the diet containing the enzyme preparation it is not known if this preparation might have given a better growth response had fermentation not occurred.

The condensed herring solubles allowed a relatively poor rate of growth as would be anticipated from the amino-acid balance of the protein going into the presswater in the reduction process (Almquist, 1949; Ney *et al.*, 1950). Carpenter and Ellinger (1955) obtained a gross protein value of 67 for condensed herring solubles as compared to values of 93 and 98 for samples of herring meal. Laksessvela (1958) likewise has reported that condensed herring solubles is of negligible value as the sole source of protein in a chick diet. Laksessvela found, however, that certain mixtures of herring solubles and herring meal were superior to meal alone. Sure and Easterling (1952) found the net utilization value of the protein from a sample of herring meal with solubles to be 73.6 as compared with a value of 69.5 for a sample of ordinary herring meal. In the present experiment there was no significant difference between the average weights of the chicks fed the presscake meal and those fed the whole meal.

The differences in the efficiency with which the diets were utilized reflected the differences in the growth response to the various supplements. The condensed herring solubles resulted in the poorest feed efficiency, the two samples of herring meal promoted high feed efficiency and the two liquid fish preparations gave intermediate values.

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Scale to Length Ratio, Age and Growth of Atlantic Salmon in Miramichi Fisheries¹

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ABSTRACT

The following quadratic equation relating fork length to scale radius is derived for Atlantic salmon taken in the Miramichi commercial fisheries:

$$L = 2.40 + 12.90S + 1.22S^2$$

where L = fork length in cm; and S = anterior scale radius in mm. The value 2.40 represents the fork length in cm of the fish when the scales first appear. Smolt transformation occurs after the young have reached an approximately similar size (about 12 cm) regardless of age. Five-year-old fish with 3 river years and 2 sea years predominate in the catch. Repeat spawners constitute only about 1/20 of the catch of salmon larger than grilse.

INTRODUCTION AND ACKNOWLEDGMENTS

THIS REPORT comprises an analysis of material gathered from Atlantic salmon (*Salmo salar*) taken in the commercial fishery in the vicinity of the Miramichi River, New Brunswick, during the month of June 1929. These Miramichi samples are also compared, for size and growth rate, with samples from the Grand Cascapedia River (Calderwood, 1928) and the Moisie River (Menzies, 1926) (Fig. 1).

It gives me pleasure to acknowledge the encouragement and assistance of Dr A. G. Huntsman, who was at that time Director of the Atlantic Biological Station, St. Andrews, N.B., of the then Biological Board of Canada, and under whose direction this work was done. I also wish to thank Messrs Frank and Robert Loggie of the A. and R. Loggie Co. of Loggieville, and Mr McNerney for assistance in obtaining the material.

I wish to acknowledge the contribution made by Dr P. F. Elson of the Fisheries Research Board's Biological Station at St. Andrews, N.B. His careful review of the paper and the addition of some of his recent findings have greatly strengthened the presentation.

¹Received for publication August 8, 1960.

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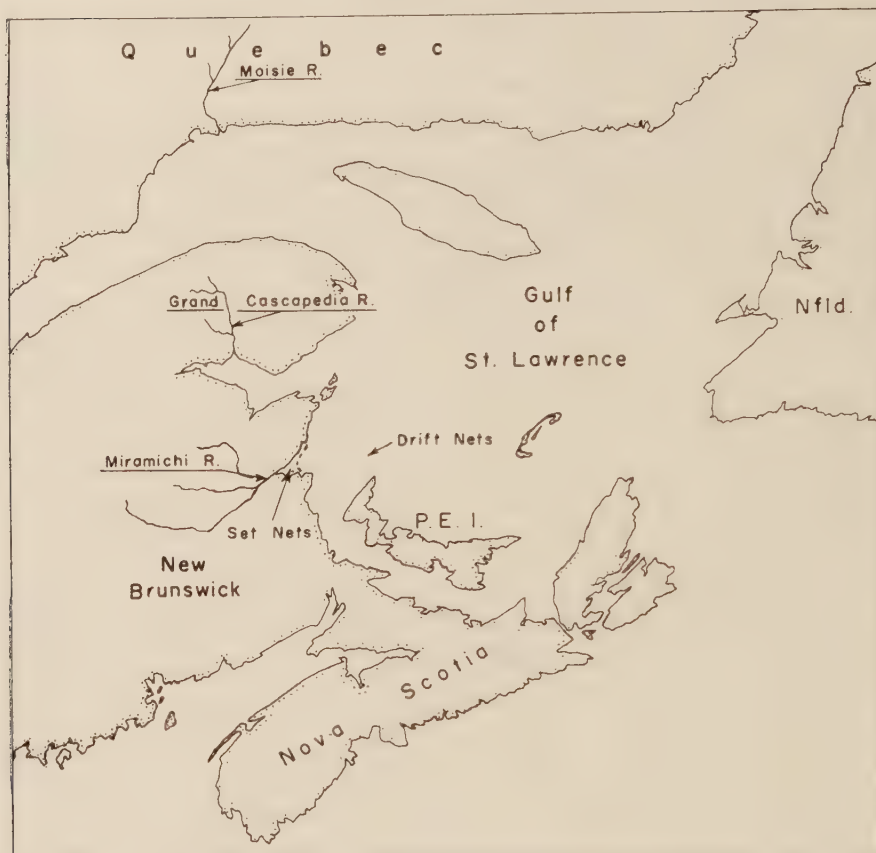


FIG. 1. The Gulf of St. Lawrence and adjoining land areas, showing three important salmon rivers, the Miramichi, the Grand Cascapedia and the Moisie. The approximate areas of the Miramichi commercial fisheries are also indicated.

MATERIAL AND METHODS

The lengths (to the fork of the tail) and weights of 436 salmon were recorded. For each of these fish about 40 scales were removed from an area just behind the dorsal fin and between the lateral line and the dorsal margin of the fish.

The scales were examined and the following facts determined: the total age of the fish, the smolt age, and the presence or absence of a spawning mark. Measurements, using a graduated micrometer disc in a microscope, were also made on 3 scales from each virgin fish to determine the final length of the anterior radius and the same radius at the end of each winter's growth.

From these measurements the length of the fish at the end of each winter's growth was determined according to the method described by Huntsman (1918).

RESULTS

SCALE LENGTHS AND FISH LENGTHS

To obtain the relationship between the scale radius and the fish length the average scale radius of 10 fish of each of several lengths was determined. The data concerning young fish was obtained from stock reared at the Miramichi hatchery. These values were plotted in a graph (Fig. 2). The relationship between the scale radius and the fork length of the salmon is parabolic and is expressed by the equation:

$$L = 2.40 + 12.90S + 1.22S^2$$

where L = fork length in cm; and S = anterior scale radius in mm.

The intercept of this curve on the L -axis at 2.40 cm nominally represents the length of the fish when the scales first appear. In point of fact, development of the scale-covering over the body of fish appears to spread progressively from primary centres of origin located along the lateral line as described for speckled trout (*Salvelinus fontinalis*) by Elson (1939). Elson found that in speckled trout

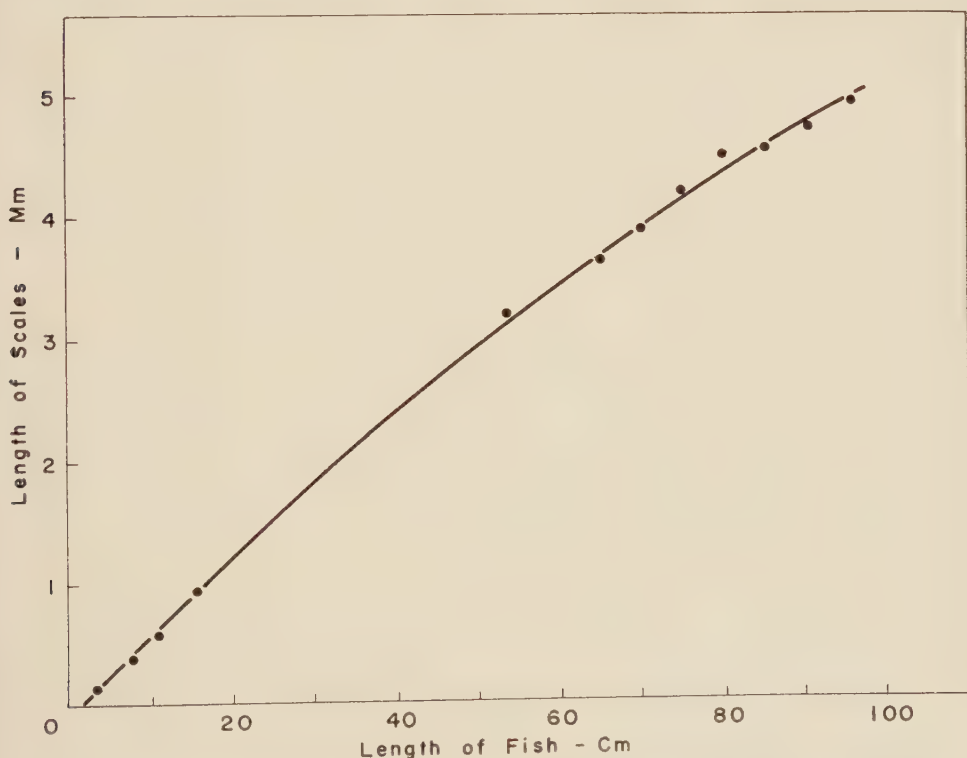


FIG. 2. The observed relationship between length of anterior scale radius (S) and fork length (L) of Atlantic salmon, as found for 436 fish taken in the Miramichi commercial fisheries in June 1929. The parabolic curve is described by the equation $L = 2.40 + 12.90S + 1.22S^2$.

the process was started at a total length (to midway between tips of tail fin when extended naturally) of about 3.0 cm and completed when the fish reached about 6.0 cm. He finds (personal communication) that for salmon the general order of scale appearance is similar to that for trout, but scale development occurs while the fish are growing from about 2.5 to 4.0 cm. He concludes that application of a correction term such as that (2.40 cm) appearing in the above equation would be a useful device for computing fish lengths from scale measurements.

In the case of the herring Sherriff (1922) found that a parabolic relationship exists between scale length and fish length (to midway between tips of tail fin when extended naturally).

AGE CLASSES

The commercial salmon fisheries carried on in the Miramichi area may be divided into two classes, that done by means of set nets within the estuary of the river and that done with drift nets outside of the estuary. Some interesting facts are revealed by an analysis of the age classes of maturing virgin fish from these two sources. Grilse (fish maturing at 1+ sea years) are not included in this analysis because no quantitative conclusions may be drawn from the number of grilse in the collection; the nets were of too large a mesh to capture the grilse in the same proportion as they took the larger salmon.

TABLE I. Sea ages of salmon taken by set nets within the Miramichi estuary and drift nets in the adjacent open sea.

Type of fishery	Winters in sea after migration as smolts			
	2		3	
	no.	%	no.	%
Set nets	208	100	0	0
Drift nets	160	85.5	27	14.5

No unspawned fish which had remained 3 years in the sea were caught within the mouth of the river, whereas 14.5% of the fish which were caught outside of the mouth of the river were fish which had remained 3 years in the sea before returning to the river. This may be explained in two ways: either the fish which have been in the sea for 3 years were not ready to ascend the river in June, or they were on their way to another river and were not going up the Miramichi River.

The lengths and weights of the various classes are given in Table II.

TABLE II. Smolt age and size of salmon taken in Miramichi commercial fisheries, June 1929.

Smolt age	2 sea winters				3 sea winters			
	Length		Weight		Length		Weight	
years	cm	in	kg	lb	cm	in	kg	lb
2	73.1	18.6	4.4	9.7	91.2	23.2	9.4	20.8
3	73.0	18.5	4.4	9.7	92.8	23.6	9.1	20.1
4	74.3	18.9	4.6	10.2	93.3	23.7	8.2	18.1

Table II suggests slightly greater length and weight when caught in the case of the fish which had stayed longer in the river as parr. There is a similar correlation in the case of the lengths of the 3-sea-winter class, but the correlation is inverse for the weights of the 3-sea-winter class; however the numbers in the 3-sea-winter class were comparatively small (Table I).

Compared with the 1926 catch in the Grand Cascapedia River (Calderwood, 1928), these Miramichi salmon were about 1 to 2 kg (2–5 lb) less in weight and about 5 cm (2 in) shorter in length, for each age group. Compared with the 1922 and 1923 catches in the Moisie River (Menzies, 1926), the Miramichi salmon were about 0.2 to 1.33 kg (0.5–3 lb) less in weight, and about 2 to 4 cm (0.8–1.6 in) shorter.

The grilse, as stated above, were not treated quantitatively. However for 15 specimens it was determined that all had spent 3 years in the river and 1+ years in the sea. The average length was 53.1 cm (20.9 in) and the average weight was 1.6 kg (3.5 lb).

SMOLT AGES AND LENGTHS

Smolt ages were determined for this collection of Miramichi salmon and compared with fish from the Grand Cascapedia and Moisie Rivers.

Compared with the Moisie and Grand Cascapedia fish (Table III), 3-winter smolts are more predominant in the Miramichi than in either of the other two rivers, 2-winter smolts are greater in proportion than in the Grand Cascapedia River but less than in the Moisie, and 4-winter smolts are less than in either of the other two streams.

TABLE III. Smolt ages of salmon (2 sea winters or more) caught in Miramichi commercial fisheries (June 1929), and by angling in the Grand Cascapedia (1926) and Moisie (1922 and 1923) Rivers, as percentages of total samples.

	Winters in river					Number of fish
	1	2	3	4	5	
	%	%	%	%	%	no.
Miramichi	0	19.3	78.2	2.5	0	436
Grand Cascapedia	0	6.0	58.8	34.1	1.1	182
Moisie	0	56.0	39.0	4.7	0.3	377

These Miramichi area salmon differ markedly from those in Scottish rivers in that there are no 1-winter smolts in this sample; this difference has also been pointed out by Calderwood (1928) in the case of the Grand Cascapedia salmon.

The lengths of the smolts at migration and the lengths of the parr before migration were calculated as described above. The average lengths are tabulated in Table IV.

The 2-winter length is 1.5 cm greater than that for the Moisie River; the 3-winter length similar and the 4-winter length 2 cm less; in comparison with

TABLE IV. Average fork lengths, at earlier stages of their life, of virgin salmon (2 sea winters or more) taken in the Miramichi commercial fisheries in June 1929, as calculated from scales removed at capture. Calculations were made according to the formula $L = 2.4 + 12.90S + 1.22S^2$, where L = fork length of fish in cm, and S = anterior scale radius in mm.

Smolt age	Length at end of winters					
	In the river				In the sea	
	1	2	3	4	1	2
<i>years</i>	<i>cm</i>	<i>cm</i>	<i>cm</i>	<i>cm</i>	<i>cm</i>	<i>cm</i>
2	5.9	11.5	...	...	45.4	66.9
3	5.2	8.6	12.0	...	44.6	71.4
4	4.7	7.5	9.9	12.9	45.5	66.9

those of the Grand Cascapedia River, the 2-winter smolts are very nearly the same length, while the 3- and 4-winter smolts are 1.5 to 2 cm less.

As shown in Table IV, fish which migrate at 2 years (2 winters) of age are longer at that age than those fish which do not migrate until they are 3 or 4 years of age; also the fish which migrate at 3 years of age are longer at that age than those fish which do not migrate until they are 4 years of age. In fact, these fish conform well with the hypothesis advanced by Elson (1957) that, in order to become smolts in the following spring, young salmon parr must reach a total length of at least 10 cm during the preceding season of growth.

CALCULATED LENGTHS AFTER MIGRATION

The lengths of the fish at the end of each winter after migration were also calculated and are included in Table IV.

Compared with the actual measurements at capture of grilse and of 2-sea-year salmon (Table II), these calculated lengths are slightly less. This is at least partly attributable to the fact that many of the fish showed, by their scales, that some growth had taken place between the end of the last winter in the sea and the time of capture.

SPAWNED FISH

In this collection there were 25 fish (5.7% of the sample) which had spawned previously. Of these fish 24 had spawned once previously and one had spawned three times previously.

The fish which had spawned once may be divided into two classes. The first class consists of those fish which had spawned first as grilse and then spent another year in the sea. These were 12 in number (2.8% of the sample); they averaged 75.5 cm (29.7 in) in length and 4.8 kg (10.6 lb) in weight. The other class consists of those which had spawned first as 2-sea-year salmon, then spent another year in the sea; these also were 12 in number, but averaged 90.5 cm (35.6 in) in length and 8.5 kg (18.6 lb) in weight.

No fish which had previously spawned twice were recorded.

The one fish which had spawned three times measured 119 cm (46.9 in) and weighed 19.1 kg (42 lb). Its scale record showed that it had been a 3-winter smolt, spawned first as a 2-sea-year salmon and thereafter in alternate years so that it was returning in its 12th year of life (age 11+).

RATE OF GROWTH

The rate of growth, to the end of the second winter at sea, is considered separately for each smolt-age group. Calculated lengths at the end of each year, for each smolt age, can be seen by inspection of Table IV, and in Fig. 3. The growth in the river is represented by that part of the curve which has a relatively

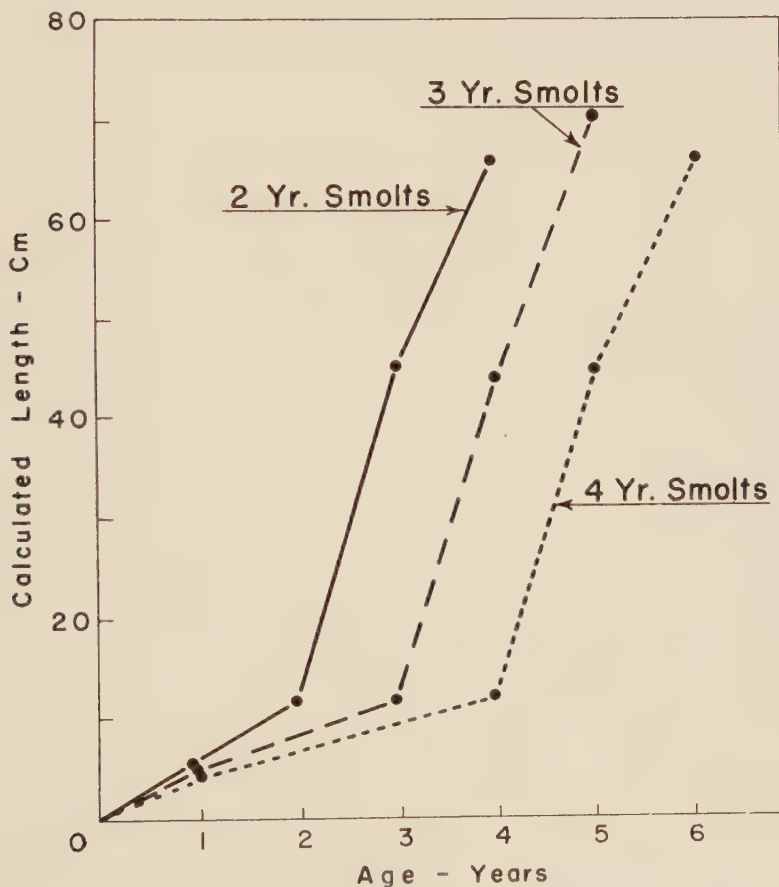


FIG. 3. Growth rates of Atlantic salmon taken in Miramichi commercial fisheries in June 1929, as calculated from scale measurements. The curves are extended only to the end of the second winter at sea, not to final length at capture which would be a little longer for 2-sea-winter fish and much longer for 3-sea-winter fish.

gradual slope, whereas the growth in the sea is represented by that part of the curve with the much steeper slope. The great difference in rate of growth in the river and in the sea is shown clearly. In each smolt-age group the increment of length added during the second year after migration is less than that added during the first year. But the rates of growth in the sea are similar for all three smolt-age groups.

SUMMARY

1. Scales of 436 salmon from the Miramichi commercial fisheries were examined and the age and other particulars were determined.

2. The anterior scale radius (S in mm) is related to the fork length (L in cm) of these Atlantic salmon by a parabolic relationship of the form $L = 2.4 + 12.90S + 1.22S^2$. The value 2.4 is a correction term which compensates for the fact that scales only begin to appear after the fish reaches a length of about 2.5 cm.

3. The predominating smolt age of these salmon was 3 years.

4. Almost 95% of this sample from the Miramichi salmon fisheries consisted of virgin fish which had spent 3 years in the river and 2 years in the sea.

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Liver Glycogen Reserves of Interacting Resident and Introduced Trout Populations¹

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ABSTRACT

Three groups of trout, two introduced populations of *Salmo gairdneri* and a resident *Salmo clarki*, were studied in stream sections. Liver glycogen deposits, which were reduced to low levels during transportation to the stream, were restored in 2 to 3 weeks in all groups, with recovery rates being approximately inverse to the population density. Within the hatchery groups, larger fish laid down greater glycogen stores. Wild trout maintained their high glycogen reserves throughout the experiment.

INTRODUCTION

RECENT INVESTIGATIONS in fish behaviour, such as those of Braddock (1949) indicating the relation between prior residence and dominance, as well as those of Newman (1956), stressing the relation between size and dominance, have led to physiological studies of trout interactions. Accordingly, Miller (1958), examining the lactic acid produced during competition between planted and resident stocks, showed that in a stream environment at least, prior residence and dominance are related. The size factor, however, has not been explained on such a basis.

Essentially a continuation of Miller's work, this study is an attempt to evaluate the responses of different-sized planted trout to interactions between themselves and resident fish. An analysis of liver glycogen stores suggests a chemical basis for the relation of size and prior residence to dominance.

THE TEST AREAS

South Gorge Creek, one of the test streams of the Alberta Biological Station, was selected for this study. Conditions were similar to those previously described by Miller (1958) for the main Gorge.

Indigenous *Salmo clarki* were confined in 3 experimental zones, each about 300 yards long, screened off by fish-proof fences. In zones 1 and 2, these fish were removed with a fish toxicant. On the basis of this poisoning, the population of the 3rd area was estimated to be about 60.

¹Received for publication March 21, 1960.

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Hatchery-reared *Salmo gairdneri* were then spot-planted into each zone. Two groups, the same lots as those of Miller *et al.* (1959), were used. In one lot, the fish had an average weight of 95.8 g and had been fed on Clark's dry rations (see Miller *et al.* for description), while in the second, fed on beef liver, the average weight was 65.6 g. Both lots of fish were the same age. The resident *S. clarki* were smaller than the fish in either hatchery group, averaging 52.8 g.

After planting, the experimental areas contained the following numbers of rainbow trout:

Section I 100 trout, 50 liver-fed and 50 Clark-fed

Section II 200 trout, 100 liver-fed and 100 Clark-fed

Section III 160 trout, 50 liver-fed and 50 Clark-fed plus 60 resident cut-throat trout.

Because of their small size, the experimental areas showed marked differences in their suitability for supporting trout populations. Hence, it was desirable in this respect to compare the zones relative to one another.

Table I summarizes the descriptive data of the experimental areas. Mean depth, width, and volumes of flow were very nearly the same, as were the values recorded for bottom fauna.

TABLE I. Description of experimental areas in South Gorge.

Section	Mean width	Mean depth	Length	Volume of flow	Bottom fauna	
					Vol./sq ft	Organisms
	<i>ft</i>	<i>ft</i>	<i>ft</i>	<i>cu ft/sec</i>	<i>cc</i>	<i>no.</i>
I	14.0 (4-24)	0.75	1000	11.6	0.7	49
II	13.0 (4-24)	0.60	1000	9.5	1.0	44
III	13.0 (4-27)	0.85	1000	10.7	0.7	50

In Table II, pools and bank cover are compared. Boussu's (1954) definition of a pool as a comparatively deep section with quiet surface waters, appreciable reduction in water velocity and with a bottom of silt or clay, was adopted.

TABLE II. Description of pools and bank cover. Length, depth and width were determined at 3 to 5 points in each pool. Each grade of bank cover is expressed as a percentage of the total bank length, to the nearest 5%. (1 yd = 3 ft = 0.9 m.)

Section	Pools				Bank cover grade		
	Total area	Mean width	Mean length	Mean depth	1	2	3
	<i>sq yd</i>	<i>yd</i>	<i>yd</i>	<i>ft</i>			
I	150	4.4	9.2	1.0	50	20	30
II	236	5.8	11.6	0.9	30	20	50
III	360	5.8	13.5	1.0	45	35	20

Borderline cases were encountered, but since all the determinations were made by the author alone, the values are probably valid relative to one another.

A comparison of relative population densities could be made by simply expressing the population in each zone as numbers of fish per unit of pool area (Table III). Section 3 is the most favourable, Section 2, the least. To check this evaluation, an analysis of bank cover was made. On the south Gorge, bank types range from steep sloping banks of sheer shale or rock to ones of

TABLE III. Number of trout per 5 square yards (4.2 m²) of pool in the experimental zones.

Section	Number
I	3.3
II	4.2
III	1.5
Wild stock areas	1.0

overhanging dense stands of vegetation, frequently with undercut fertile edges. Hence, evaluation of cover in the 3 zones was possible only by arbitrarily establishing grades of bank types. These were defined as follows:

- Grade I Vegetation overhanging water, supplying food and cover.
- Grade II Bank vegetation separated from the water by only a short distance (up to 3 yards—2.7 m); or, no bank vegetation, but overhanging rocks, logs, etc., supplying good cover.
- Grade III No vegetation or other cover. Bank of rocks, boulders, shale and/or gravel.

Bank vegetation included:

<i>Salix</i> sp.	<i>Vicia</i> sp.	<i>Anemone</i> sp.
<i>Populus tremuloides</i> Michx.	<i>Juncus</i> sp.	<i>Pyrola</i> sp.
<i>Populus balsamifera</i>	<i>Epilobium angustifolium</i> L.	<i>Ribea</i> sp.
<i>Picea glauca</i>	<i>Epilobium latifolium</i> L.	<i>Lonicera</i> sp.
<i>Picea mariana</i>	<i>Actaea rubra</i> (Ait.) Willd.	<i>Aster</i> sp.
<i>Juniperus horizontalis</i> (Moench)	<i>Heracleum lanatum</i> Michx.	<i>Senecio</i> sp.
<i>Pinus contorta</i> Dougl.	<i>Taraxacum</i> sp.	<i>Achilles</i> sp.
<i>Rosa</i> sp.	<i>Betula</i> sp.	<i>Equisetum</i> sp.
<i>Potentilla fruticosa</i> L.	<i>Campanula</i> sp.	<i>Shepherdia</i> sp.
<i>Fragaria</i> sp.	<i>Castilleja</i> sp.	<i>Elaeagnus</i> sp.
<i>Lathyrus</i> sp.	<i>Habenaria</i> sp.	<i>Deschampsia</i> sp.
<i>Hedysarum</i> sp.	<i>Carex</i> sp.	

Table II shows that the test zones differed primarily in the amount of bank grades 1 and 3. Sections 1 and 3 were similar, both being superior to Section 2. This rating is in fair agreement with that based on total pool areas and suggests that fish would be expected to do better in Section 1 or 3 than in Section 2, while, because of density differences, Section 3 fish would be expected to do better than

those in Section 1. This expectation is considered in evaluating the experimental results.

METHODS

Each fish was marked with a numbered Petersen tag in the Calgary Hatchery, about one week prior to planting. During transportation from the hatchery, water was continually oxygenated, and the fish were maintained at low densities, to keep them in good condition. The trout were carried to the stream in large 30-gallon cans and spot planted. During the experiment the fish were recaptured either by angling or seining.

Liver examples were taken from a few fish of each lot on arrival at the experimental area. After this, sampling was carried on at the end of the 1st, 2nd, 3rd and 4th weeks after planting. Samples were placed directly into weighed capped test tubes containing 30% potassium hydroxide. These were re-weighed at the laboratory and the dissolved tissues were analyzed for glycogen by the method of Montgomery (1957). All trout used were killed within 30 seconds of capture by decerebration. Tissue sampling was completed within about 60 seconds after capture.

Stomach samples were collected, weighed and compared relative to total body weights.

Stream descriptive data were collected upon completion of the experiment, i.e. in early September. Plant identification, rendered difficult because of the time of the year, was based on Budd's key (1957). Stream description was patterned after Lagler (1957).

RESULTS

DISTRIBUTION OF HATCHERY TROUT FOLLOWING PLANTING

Within 24 hours after planting, each trout group had dispersed throughout the experimental areas. Trout were most conspicuous in Section 2 and in the pools very near to the downstream screens of each of the other sections.

In all zones, during the first few days, trout were frequently seen resting vulnerably in very shallow, slow moving waters. Again the number visible was greater in Section 2 than in the other sections.

WEIGHT CHANGES AFTER PLANTING

Table IV summarizes the weight changes after planting, expressed as a percentage amount less than the weight at planting. Differences between the diets were not large, though the smaller trout tended to lose relatively more weight in most areas. Initial loss rates were much the same under all densities. However, Section 3 trout under the lowest population density showed lower weight losses than both the other lots. This was especially pronounced at 2 and 4 weeks after planting. When the data are treated irrespective of diet, the Section 3 fish showed the lower weight loss consistently.

TABLE IV. Weight changes after planting, expressed as percentage decrease from planting weight.

Section	Lot	Days after planting			
		6-8	13-15	20-22	27-29
III	Clark-fed	16.4	15.3	19.0	15.2
	Liver-fed	16.4	19.5	21.2	16.9
	Average	16.4	17.4	20.1	16.1
I	Clark-fed	16.8	16.5	24.8	16.3
	Liver-fed	15.7	20.7	22.8	19.0
	Average	16.2	18.6	23.8	17.6
II	Clark-fed	15.6	18.1	23.1	21.1
	Liver-fed	18.7	23.1	23.4	24.2
	Average	17.1	20.6	23.3	22.7

THE STOMACH CONTENTS OF HATCHERY AND WILD TROUT

If stomach content can be used to indicate trout feeding, then Table V shows most clearly the superiority of the resident wild *S. clarki*. Within the hatchery groups, feeding increased gradually after planting. Large Clark-fed trout began feeding more actively than the liver-fed group within the first week

TABLE V. Weight of stomach contents, expressed as a percentage of body weight, for native *Salmo clarki* and planted *S. gairdneri*. (Numbers in brackets refer to number of stomachs examined.)

A. Wild <i>Salmo clarki</i>				
Days before planting				
	28	21	14	2
South Gorge Creek	1.10 (9)	2.59 (4)	1.51 (6)	1.07 (5)
Days after planting				
	6-8	13-15	27-22	27-29
South Gorge Creek	1.03 (3)	0.94 (4)	1.00 (5)	0.81 (5)
B. Hatchery <i>Salmo gairdneri</i>				
Days after planting				
	6-8	13-15	20-22	27-29
SECTION I				
Clark-fed	0.12 (5)	0.07 (4)	0.13 (3)	0.18 (4)
Liver-fed	0.19 (5)	0.07 (4)	0.19 (3)	0.19 (4)
SECTION II				
Clark-fed	0.05 (5)	0.05 (3)	0.16 (5)	0.42 (5)
Liver-fed	0.02 (5)	0.07 (3)	0.21 (4)	0.46 (3)
SECTION III				
Clark-fed	0.24 (4)	0.34 (4)	0.28 (4)	0.63 (4)
Liver-fed	0.15 (4)	0.13 (4)	0.24 (4)	0.35 (4)

and this was maintained for the duration of the experiment. The trout subjected to the highest population densities showed slowest increase in ability to take in food.

LIVER GLYCOGEN RECOVERY AFTER PLANTING

Data dealing with glycogen reserves in the liver of the planted trout are summarized in Table VI. Since no substantial variations were seen in the liver glycogen levels of wild *S. clarki* throughout the study period, their values were

TABLE VI. Liver glycogen of hatchery *Salmo gairdneri*, before and after planting, in grams per 100 g of tissue, with standard errors.

Lot	At planting	Days after planting			
		6-8	13-15	20-21	27-29
Clark-fed					
Section III	1.20 ± 0.17 (5)	2.40 ± 0.34 (4)	3.59 ± 0.34 (4)	3.50 ± 0.45 (4)	3.28 (4)
Section I	As above	2.01 ± 0.43 (5)	2.92 ± 0.07 (4)	3.31 (3)	3.17 (4)
Section II	As above	1.76 ± 0.15 (5)	2.16 ± 0.11 (3)	3.13 (4)	3.03 (5)
Combined	As above	...	...	3.32 ± 0.21 (11)	3.15 ± 0.20 (13)
Liver-fed					
Section III	0.60 ± 0.21 (5)	2.00 ± 0.35 (4)	2.73 ± 0.42 (4)	2.59 ± 0.46 (4)	2.67 (4)
Section I	As above	1.82 ± 1.9 (5)	1.75 ± 0.16 (4)	2.15 (3)	2.37 (4)
Section II	As above	1.26 ± 0.19	1.49 (4)	2.02 ± 0.12 (4)	2.90 (5)
Combined	As above	...	...	2.26 ± 0.18 (11)	2.65 ± 0.14 (13)

lumped into two categories, those before the onset of the experiment and those after: the pre-experiment average is 4.57 g/100 g tissue, with standard error of 0.38, based on 20 fish taken over 4 weeks; the average figure during the experiment is 4.41 ± 0.18 , based on 19 fish.

The most striking fact arising from Table VI is that the wild trout liver glycogen levels are maintained above those of the planted rainbow trout throughout the entire period.

Perhaps the most significant difference between the experimental zones were the rates of recovery following planting. Clark's trout at lowest densities (Section 3) increased their liver glycogen reserves by about 200% within 2 weeks; those in Section 1, by about 160%; while Clark's trout in the densely populated Section 2 showed only about 75% increase in this time.

Liver-fed fish, probably because initial levels were somewhat lower, recovered at a rapid rate during the first week; those in Section 1 and 3 showing about 180%

increases, while the lot in Section 2 showed only 70% rises. During the second week, the recovery rate was reduced.

In both liver- and Clark-fed trout at low densities, peak liver glycogen deposits were achieved a fortnight after planting. The trout in the other two zones, however, irrespective of diet, did not show maximum deposition until the third week after planting. This is most striking, especially in view of the fact that very large increases in liver glycogen can occur quickly with good feeding (Hochachka, unpublished).

Since liver glycogen levels were the same in all Clark-fed trout on arrival at the experimental areas (i.e. at planting), it is not surprising that differences between trout planted in the different zones were not statistically different until a 2-week period elapsed. At this time, deposits were significantly higher in trout living at lower densities (Section 1 and 3) than they were in those at high density.

By 3 weeks after planting, differences between the different density zones were again obliterated. Since the trout were on the same natural diet, this was to be expected. However, the liver glycogen levels of the hatchery trout at 3 and 4 weeks are significantly lower than those of the resident *S. clarki*. Moreover, the larger Clark-fed fish had significantly higher levels than the liver-fed ones (at 3 weeks, $P=0.01$, but by the 4th week this difference was reduced to the 0.05 probability level).

In sum, restoration of liver glycogen reached the maximum observed within 3 weeks. After this time, *within each dietary lot*, glycogen stores remained the same, irrespective of population density. However, larger hatchery trout achieved greater glycogen deposition than smaller ones. Wild trout in Section 3 maintained significantly higher reserves of liver glycogen than their hatchery counterparts, in spite of the fact that both were subjected to the same conditions.

RELATIONS BETWEEN TROUT GROUPS

Two approaches were used to obtain direct evidence for the presence of social orders; observations of activity within secluded stream portions, and feed-lot and/or size sequences in capture by angling.

Time sequences of capture within given pools indicated that feeding among the resident cutthroat trout was based largely on size, the larger fish being first to attempt to capture the food presented. This generalization did not hold true in the mixed populations, where the smaller wild stock fed more actively than their hatchery counterparts. Within the hatchery stocks, however, feeding was also related to size.

Except for several well-suited pools, observations of movements were difficult. Those that were made can be summarized as follows: 1. Freedom of movement was greater among the resident trout. 2. Wild trout went to deep, dark, and well protected parts of the pools when inactive; hatchery trout swam

very close to the surface, often in shallow water. 3. Wild trout frequently molested introduced ones, but were seldom molested themselves. This behaviour of the wild trout is similar to the activity of the dominant trout in Newman's (1956) study.

DISCUSSION

WEIGHT LOSS AFTER PLANTING

Weight data are similar to those recorded in the literature. Miller (1951) reported about 20% losses in weight in 3-year-old planted trout, while 2-year-olds showed up to 65% decreases. In 1953, Miller noted that whereas 3-year-old pond-reared trout lost up to 20% of their weight at planting, stream-reared stock lost only 12% at maximum, and transplanted wild stock lost only 9%. Since the greatest drop in weight occurred during the first week or so, both in this and in Miller's studies, it is likely that starving was most serious during this time. Quick returns to normal weight ranges probably were postponed in favour of the utilization of energy from food intake for firmer establishment in the stream social structure.

Differences between diets were not apparent despite size differences, and the scatter between zones was so large that differences were not statistically valid. It is, therefore, concluded that weight changes can be used only as a crude index of the responses of fish to varying degrees of environmental stress.

LIVER GLYCOGEN

Liver glycogen levels are considered to be biochemical reflections of food intake, and as Fig. 1 shows, these vary approximately with the latter. This is further substantiated by Miller *et al.* (1959) as well as by data from the author's unpublished feeding experiments. Since these reserves quickly increase with food intake, and since all the trout were presumably taking the same type of food, dietary histories *per se* are assumed of little importance after the first week under natural conditions.

The smaller hatchery fish tended to have lower liver glycogen deposits for a given amount of food intake (see Fig. 1). This is probably spurious, for these energy deposits are highly labile, and are easily influenced by other factors, most notably, physical activity (Hochachka, unpublished; Miller *et al.*, 1959). It is probable that the lower glycogen deposition of the liver-fed trout is due to their stream position, which according to Miller (1958) would be inferior to that adopted by dominant fish.

It should be pointed out that the experimental hatchery trout were transferred for some 60 miles from the hatchery to the experimental stream. Liver glycogen levels at this time were about 20 to 25% of those normally seen, and differences between the diets were not significant.

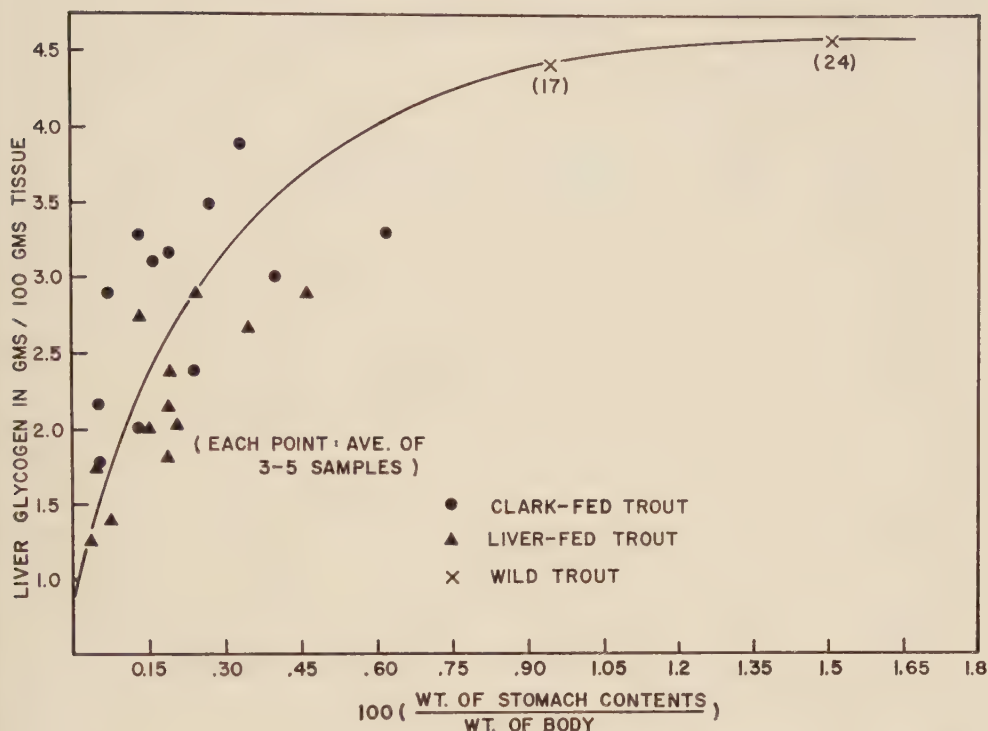


FIG. 1. Liver glycogen reserves per unit weight of tissue, plotted against stomach contents (as percentage of body weight), for all samples of planted *Salmo gairdneri* and wild *S. clarki*. The 24 wild fish are those taken prior to planting the hatchery trout; the 17 were taken after planting.

DOMINANCE-SUBORDINATION ORDERS

In his laboratory and field studies of trout behaviour, Newman (1956) found that rainbow trout portray a loose sort of rotating dominance-subordination relation in which "nip-right" and reciprocal aggressiveness prevail. Aggressiveness became more severe during feeding, and if the subordinate fish were subjected to intense domination, they frequently failed to feed at all. This is especially important to a behaviour interpretation in this study, because of the direct relation between food intake and liver glycogen stores. Stringer and Hoar (1955) recorded two predominant patterns of behaviour in the trout social structure—chasing and nipping, with territorial defence, threatening, and fighting being associated with nipping. In both studies, the hierarchy was usually based on size.

If the trout groups in this study are arranged in order of merit on basis of liver glycogen stores, stream position, feeding, and other activity, the following sequence arises: wild stock > Clark-fed > liver-fed. The size sequence, of course, was: Clark-fed > liver-fed > wild stock. That is, all the evidence points to *wild-stock dominance despite size disadvantage*. Mortality data (Miller, 1958; unpublished data from this study), Phillips' *et al.* (1957) chemical data, as well as

unpublished results in the present writer's study of fish performance also support the above implication.

This contradiction of the size factor in dominance-subordination orders probably has two contributing factors:

(a) *Prior residence.* The importance of this factor has been experimentally demonstrated by Braddock (1949) and Miller (1958). The former showed that prior residence actually competes with the size factor in determining dominance, while the latter indicated the especial significance of prior residence in hatchery fish survival, as well as certain biochemical consequences. In this study, prior residence was, for at least 4 weeks, more important than size in determining dominance.

(b) The second factor could be a *less healthy condition of the larger hatchery fish*. Evidence for this is seen in the glycogen levels recorded as well as in Miller's lactic acid data. It is some such condition that Miller suggested as instrumental in delayed mortality.

Newman (1956), too, held that where dominance was acquired by smaller trout, it was due to the body state of the larger protagonist, and this worker recognized the other possible alternative as well, viz., that the smaller fish were more aggressive. The latter alternative could not be assessed in this study.

Finally, greater activity of dominant fish points to one of the rewards of dominance; selection of territory within a home range. (See Miller, 1954, 1957, for a discussion of trout home ranges). But increased activity also implies that the position of advantage is frequently relinquished, thus giving rise to Newman's rotating social structure. In essence, this is a sharing of the desirable position and is undoubtedly of value to the social group as a whole.

SUMMARY

1. The body weight changes and feeding activity of hatchery-reared rainbow-trout following stream planting were roughly related to the population density to which the fish were subjected.
2. Restoration of liver glycogen after planting reached the maximum observed within 2 to 3 weeks. After this time, within each dietary group, these stores were the same, irrespective of population density, but higher levels were obtained by larger trout.
3. Wild cutthroat trout, despite a size disadvantage, maintained higher liver glycogen reserves than did hatchery fish.
4. Liver glycogen depots were reduced to very low levels during transportation to the stream. At planting, the levels were the same in both dietary lots.
5. Interpreted on the basis of known patterns of behaviour, the small wild trout were dominant to the larger hatchery ones. This size discrepancy was probably due to a less healthy state of the hatchery fish and/or to the prior residence of the wild stock.

ACKNOWLEDGMENTS

This work is dedicated to the late Dr R. B. Miller, friend and professor to the author.

It is a pleasure to extend especial gratitude to Mr. A. C. Sinclair, Superintendent of the Alberta Trout Hatchery, who tagged, weighed, and transferred the experimental trout, and to a fellow student, Mr D. Fillion, who aided in stream work.

Thanks are also extended to the National Research Council of Canada, whose bursary supported the project and to the Directors of the Alberta Biological Station, who made the project possible.

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Slicing of Fillets as an Aid in Detection and Removal of Codworms from Atlantic Cod Fillets¹

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ABSTRACT

Slicing cod fillets longitudinally into slices $\frac{1}{2}$ inch (13 mm) thick can increase the efficiency of candling cod fillets for codworms to over 95%. The increase is greater in the larger fillets than in the smaller fillets if sliced. If fillets are not sliced the candling efficiency decreases with increasing size of fillets.

INTRODUCTION

DETECTION OF CODWORMS (*Porrocaecum decipiens*) in fillets is very difficult when they are further than $\frac{1}{4}$ inch below the surface of the fillet (Power, 1957). In an attempt to improve methods of detecting these parasites for the purpose of removing them, experiments were conducted to determine the effect on the efficiency of candling the fillets, after slicing them longitudinally, parallel to the skin surface, into layers with a maximum thickness of $\frac{1}{2}$ inch (13 mm) as shown in Fig. 1. The slicing was effected by means of a slicing machine designed by the

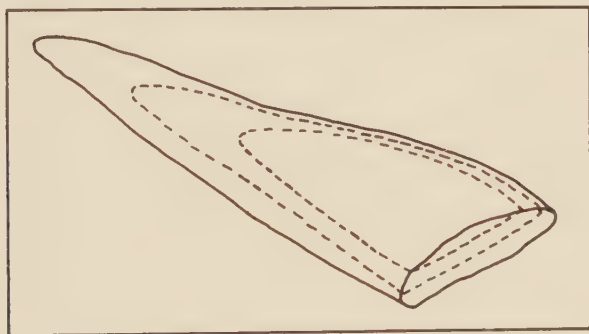


FIG. 1. Typical cuts made when a cod fillet is sliced for candling.

author at this Station (Power and Fougère, 1960). The machine employed four band knives crossed to form a figure "8", running on the same two pulleys. The blades were spaced $\frac{1}{2}$ inch apart by means of steel guides. Fillets were fed to the blades by a conveyor belt. For these experiments heavily infested cod fillets were used.

¹Received for publication October 13, 1960.

Table I shows the results of slicing and candling 228 heavily infested cod fillets. First both sides of these fillets were candled under conditions similar to those under which fillets are candled commercially and the number of parasites was recorded. The fillets were then cut into slices $\frac{1}{2}$ inch thick and again both sides were candled and the number of additional parasites found was recorded.

TABLE I. Results of candling, slicing and again candling 228 cod fillets.

Size of fillet	Number of samples	Parasites found before slicing		Additional parasites found after slicing	
		Range	Av. per fillet	Range	Av. per fillet
Large	27	0- 2	0.223	0-12	1.26
Medium large	59	0-14	2.2	0-10	1.40
Medium	81	0- 8	1.04	0- 6	0.51
Small	61	0-18	2.54	0-11	0.156
Total number of fillets 228					
Number of fillets containing parasites 153 (67%)					
Total number of parasites removed 644					
Number of parasites found before slicing 375 (58%)					
Number of worms found after slicing 269 (42%)					
Average number of worms per fillet 2.82					

Table I shows that of the 644 parasites removed from the fillets, 269 (42%) were removed after slicing, having been invisible during normal candling. The percentage of infested fillets in this group (67%) is considerably higher than the mean percentage of infested fillets from fish taken from the banks off the south coast of Nova Scotia. Scott and Martin (1957) report that 5 to 24% of such fish are infested.

To determine the effect of fillet size on the efficiency of candling sliced cod fillets, three batches of fillets were candled under commercial candling conditions, identical to those under which the fillets referred to in Table I were candled. Forty pounds of small fillets (average weight 0.55 lb), 40 lb of medium fillets (average weight 0.77 lb), and 40 lb of large fillets (average weight 1.14 lb) were candled and the numbers of parasites removed were recorded. These fillets were then sliced into layers as shown in Fig. 1 and the additional parasites removed were recorded. After the second candling, the fillets were shredded by hand to determine the number of parasites which had remained undetected.

Candling efficiency may be stated by the expression:

$$\frac{\text{Number of parasites detected by candling} \times 100}{\text{Total number of parasites}}$$

The candling efficiency for these small, medium, and large fillets is shown in Table II. For small fillets the candling efficiency is shown to increase from 26.9 to 95.4% by slicing the fillet. Residual worms were 4.6% of the total or 20 per 100 lb of fillets. For medium-size fillets the candling efficiency increases

TABLE II. Results of candling, slicing and again candling 40 lb of three typical sizes of cod fillets.

	Small	Medium	Large
Number of fillets	73	52	35
Average weight of fillets (pounds)	0.55	0.77	1.14
Range of parasites found in fillets before slicing	0- 4	0-14	0- 9
Range of parasites found in fillets after slicing	0-15	0-38	0-34
Range of residual parasites	0- 2	0- 1	0- 2
Total number of parasites found in fillets	175	223	306
Number of parasites found before slicing	47 (26.9%)	54 (24.2%)	68 (22.2%)
Number of additional parasites found after slicing	120 (68.5%)	163 (73.1%)	231 (75.5%)
Total number of parasites after slicing	167 (95.4%)	217 (97.3%)	299 (97.7%)
Number of residual parasites available	8 (4.6%)	6 (2.7%)	7 (2.3%)
Total parasites per 100 lb fillets	438	560	765
Residual parasites per 100 lb fillets	20	15	17.5
Candling efficiency before slicing =	$\frac{47 \times 100}{175}$ = 26.9%	$\frac{54 \times 100}{223}$ = 24.2%	$\frac{68 \times 100}{306}$ = 22.2%
Candling efficiency after slicing =	$\frac{167 \times 100}{175}$ = 95.4%	$\frac{217 \times 100}{223}$ = 97.3%	$\frac{299 \times 100}{306}$ = 97.7%

from 24.2 to 97.3% when the fillet is sliced, with residual worms 2.7% of the total of 15 per 100 lb of fillets. The candling efficiency for large fillets increases from 22.2 to 97.8% when candled after slicing. The percentage of residual worms in this case was 2.3% of the total or 17.5 per 100 lb of fillets.

In Fig. 2 the candling efficiency has been plotted against weight of fillets

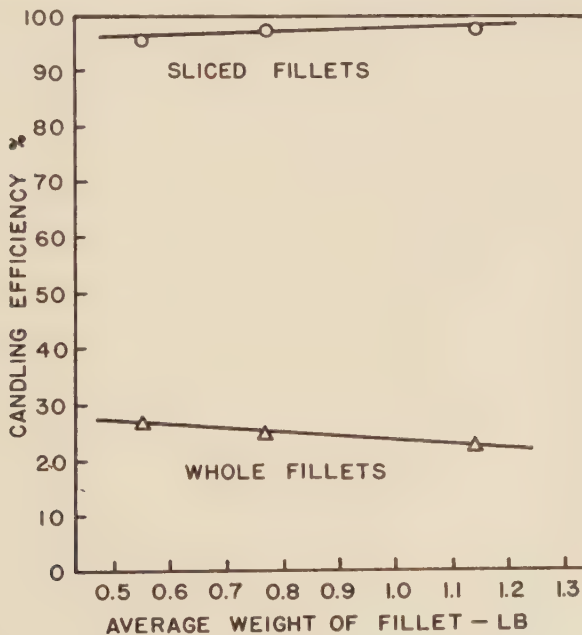


FIG. 2. Curve showing variation in candling efficiency with size of sliced and unsliced fillets.

for unsliced fillets and for sliced fillets. As can be seen the candling efficiency for sliced fillets is much greater than that for whole or unsliced fillets and tends to increase as the size and thickness of the fillet increases. With unsliced fillets the candling efficiency tends to decrease with increase in size of fillet.

A small number of parasites, less than 5%, will not be detected even if the fillets are sliced before candling, being hidden in the brown-coloured flesh of the fillet, or under the silver bloom which remains on part of the fillet after skinning. However, it is believed that they are harmless to man and this belief is borne out by the results obtained by feeding *Porrocaecum* to beagle pups as part of their diet (Crampton *et al.*, 1960).

SUMMARY

When heavily infested cod fillets are candled under commercial conditions for parasites, it can be expected that only a quarter of the total number of parasites will be found and removed. However, if the fillets are cut into slices $\frac{1}{2}$ inch thick and candled, it can be expected that over 95% of the parasites will be found.

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NOTES

Northward Range Extension of the Flathead Chub and Trout-perch to Aklavik, N.W.T.

Seine hauls in the Peel Channel of the Mackenzie River delta at Aklavik ($68^{\circ} 13.5' \text{ N Lat.}, 135^{\circ} 00' \text{ W Long.}$), Northwest Territories, Canada, produced two species north of their recorded range, the flathead chub (*Platygobio gracilis*) and the trout-perch (*Percopsis omiscomaycus*). The northernmost record in the Mackenzie system for these species was at Fort Good Hope in the Mackenzie River, more than 200 miles southeast of Aklavik by air (V. C. Wynne-Edwards, *Bull. Fish. Res. Bd. Canada*, No. 94, 1952). The trout-perch has also been collected closer to Aklavik but in the Yukon River system, at Old Crow, Porcupine River, $67^{\circ} 40' \text{ N Lat.}$ (Wynne-Edwards).

Accompanying these two species in the seine hauls were the lake chub (*Couesius plumbeus*) and the spoonhead sculpin (*Cottus ricei*), both recorded only once without definite locality from the delta, and also the longnose sucker (*Catostomus catostomus*) and several young coregonids. These fish are catalogued as NMC60-455 in the fish collection of the National Museum of Canada. The fish were seined in muddy water, 0-1.5 feet deep, 13.0° C , mud bottom on July 12, 1960, by the author and J. Bray of the Fisheries Research Board, while the former was associated with the Board's 1960 program of the M.V. *Salvelinus*.

Temperature would not appear to greatly limit northward distribution in the Mackenzie since it brings warm water north from southern regions, and winter temperatures descend no lower near its mouth than near its source. Hence these and other species might be expected to extend to within tidal influence at the mouth of the Mackenzie.

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Received for publication September 19, 1960.

Lipid Hydrolysis in Frozen Cod Muscle¹

Protein denaturation in frozen cod muscle is accompanied by a marked increase in the free fatty acid content of the tissue and it has been suggested that the two processes may be related (Dyer and Fraser, 1959). This communication is a preliminary report of studies undertaken to establish the identity of the precursors of the liberated fatty acids. The work is part of a program designed to elucidate a possible relation between lipid hydrolysis and protein denaturation in frozen fish muscle.

In stored frozen cod, the free fatty acid content often amounts to more than 50% of the total extracted lipid (Dyer and Fraser, 1959). Garcia *et al.* (1956) found that cod muscle lipid contained 50 to 65% phospholipid whereas only 3% was triglyceride. The other fatty-acid-containing constituents, cholesterol esters and "unidentified lipids", corresponded to 5 and 21% of the total lipid respectively. Therefore, phospholipid hydrolysis must be responsible for at least part of the increase in free fatty acid. Furthermore, Cardin and Bordeleau (1957) and Cardin *et al.* (1958) found that phospholipids were hydrolysed during the preparation of salt cod, and recently Lovern *et al.* (1959) reported the same occurrence when cod was kept in ice for prolonged periods. However, Tomlinson *et al.* (1960) did not observe statistically significant phospholipid breakdown in lingcod muscle held for a comparatively short time at 0°C. Olley and Lovern (1960) have concluded that phospholipid hydrolysis in cod flesh stored at various temperatures was due to tissue enzymes.

Preliminary analyses of the lipids from fresh cod and from various samples of stored frozen cod showed that the free fatty acid content increased during frozen storage and that there was a simultaneous decrease in phospholipid content.

The lipid changes associated with frozen storage were subsequently studied in more detail using silicic acid chromatography and paper chromatography. Cod muscle lipids were separated into seven distinct components (Fig. 1), which by chemical and chromatographic analysis have been identified as follows:

Component I: esterified cholesterol and probably other sterol esters; also hydrocarbons, waxes and alcohols;

Component II: free fatty acids and triglycerides;

Component III: free cholesterol and other sterols;

Component IV: unidentified phospholipid (contains phosphorus and nitrogen but no serine, ethanolamine, inositol or choline);

Component V: phosphatidylethanolamine;

Component VI: mixture of phosphatidylserine and phosphatidylinositol;

¹A preliminary account of this work was presented at the 43rd Canadian Chemical Conference of the Chemical Institute of Canada, Ottawa, June 15, 1960.

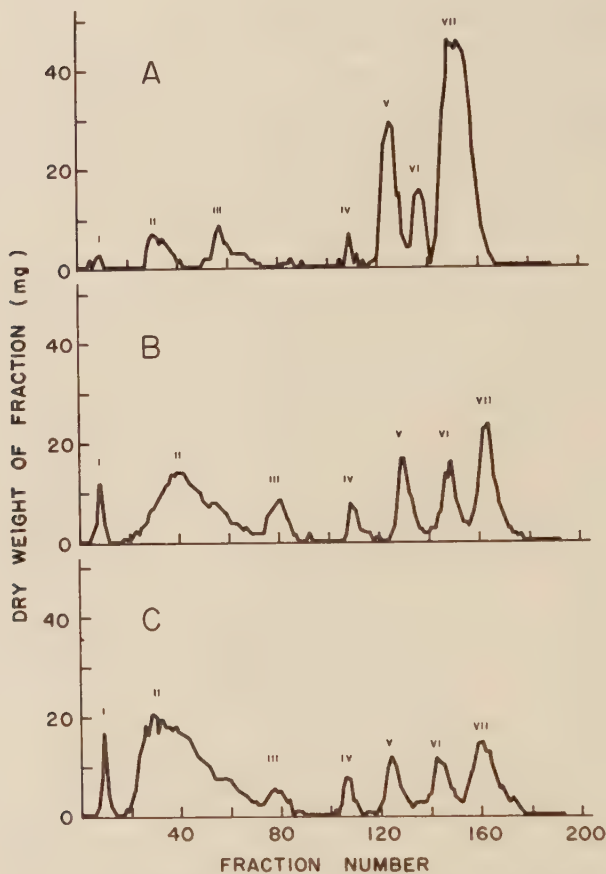


FIG. 1. Silicic acid chromatography of cod muscle lipids extracted with chloroform-methanol (Bligh and Dyer, 1959). Approximately 1 g lipid was applied to each column (50 g), followed by gradient elution with *n*-hexane→chloroform→methanol. Fractions of 10 ml each were collected. Curve A was obtained for lipids extracted from pre-rigor cod muscle (600 ml *n*-hexane and 500 ml each of chloroform and methanol used for elution); Curve B, cod muscle stored at 10°F for 7 weeks (600 ml of each solvent used for elution); Curve C, cod muscle stored at 10°F for 37 weeks (600 ml of each solvent used for elution).

Component VII: phosphatidylcholine and a much smaller amount of sphingomyelin.

The chromatograms indicate that hydrolysis of phosphatidylethanolamine and phosphatidyletholine was mainly responsible for the increase in free fatty acids in the frozen samples. Phosphatidylserine and phosphatidylinositol apparently were not affected.

It is noteworthy that the phospholipid components of the fresh cod sample (Curve A, Fig. 1) amounted to 83% of the total lipid, and also that the phosphatides containing serine, inositol and sphingosine were present in appreciable quantities.

This and more recent work will be amplified by experimental and quantitative data in a forthcoming publication.

ACKNOWLEDGMENT

The author is indebted to Dr W. J. Dyer of this Station for suggesting the problem and for his interest and helpful criticism throughout the investigation, and to Mr G. J. Jewell for technical assistance.

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Received for publication December 13, 1960.

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Artificial Drying of Cambodian Fish¹

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ABSTRACT

Through the direction of the Colombo plan, a request was received to study the possibility of artificial drying for Cambodian fish and also to design a dryer which could be used economically under the adverse atmospheric conditions prevailing in tropical countries. Various samples were sent from Cambodia to this Station for tests. It was found possible to dry this fish artificially at a good drying rate without any difficulty. A drying temperature of 110°F (43°C) can be used without any injury to the product. According to atmospheric data supplied by the weather bureau, the dew point of the air in Cambodia is always between 72.5 and 77°F (22 and 25°C), so that artificial drying is possible there without costly dehumidifying apparatus. As a result of these important findings an experimental dryer of 2-ton (1800-kg) capacity was designed. The dryer is very simple and economical and will be used in Cambodia for judging, according to local market requirements, the quality obtained; also for determining the efficiency of a possible future big unit which will include six sections similar to the 2-ton trial unit.

INTRODUCTION

THE FRESHWATER FISHERIES of Cambodia are very important for the local economy as well as for the nutrition of the local population. Various species are encountered including oily and non-oily fish. Some are very small (3 to 4 inches or 7.5 to 10 cm long), others are about the size of a medium Canadian codfish. The fish are caught in huge quantities during very short time intervals so that the available supply often exceeds the facilities for disposal by the fresh fish trade. Moreover, the captures are often made in locations far away from the centres of the fresh fish trade, or during a season in which transportation is handicapped. Therefore a substantial part of the catches has to be used for the dry fish industry.

CAMBODIAN PROCESSING METHODS

Heads and entrails are removed. Then the fish are split, washed, salted and finally dried in the sun on bamboo flakes. Some species are soaked during 16 hours in vats before being split and salted. This operation expands the tissues and allows a certain degree of fermentation, which is considered a desirable feature on account of flavour developed thereby.

When the vicinity of the fishing grounds enjoys a fair amount of sunshine, a good breeze and a low relative humidity, a stable dried product is obtained within 48 hours. The product is then shipped to the Central Co-operative

¹Received for publication September 8, 1959.

warehouse at Russey Keo near Phnompenh. At these headquarters, a final drying operation, requiring only 6 hours if the weather is suitable, takes place. The product thus obtained is exported.

Under ideal conditions, this reasonably efficient procedure is economical, but only because the cost of labour is very low. However, ideal conditions do not prevail all year round because the rainy season, during which 25 to 30% of the catches are made, lasts about 4 months. In fact, during the rainy season it takes about 3 days at the central warehouse to finish drying the fish and considerable losses are encountered by the fishermen. The greatest trouble arises from a reddening which develops on salted fish when exposed to moisture and rain. The fish so attacked cannot be exported and has to be sold on the local markets for what it will fetch.

It has been suggested that these various difficulties could be overcome by a suitable artificial drying procedure. Through appropriate channels, the Colombo Plan was approached for help by the Co-operative of Cambodia in the solution of the drying problems. The request was passed on to the Fisheries Research Board of Canada, which assigned this Technological Station to study experimentally the feasibility of artificial drying under the adverse conditions that sometimes prevail, as explained above, and also to design an apparatus for that purpose.

GENERAL CONSIDERATIONS

The first step consisted of a series of conferences with Mr Louis Bérubé, officer of the Colombo Plan, who had spent several months in Cambodia. He was able to supply much useful information concerning the difficulties encountered with the various types of fish, methods of handling, and atmospheric conditions prevailing there. The details supplied offered promise that the fish could be dried successfully by artificial means. But the difficulty was to develop a procedure and to design an apparatus which would be suited to such a cheap product under tropical conditions. Two dryers have already been installed in the East; one in Hong Kong and the other one in Colombo, Ceylon. Both dryers, however, are equipped with dehumidifying equipment and the drying operation is conducted at about the same temperature (80°F or 27°C) being used here in Canada for the preparation of various types of salt fish.

Sun drying requires only labour, which is very cheap in tropical countries, so that the use of a dehumidifying system in conjunction with an artificial dryer might not prove competitive. The removal of water from the air is usually accomplished either by refrigeration or by chemical absorption. Both systems are costly to install and expensive to operate. Improvements in these respects are to be expected in the future; however, for the present our efforts have been directed at obtaining satisfactory results without the use of external dehumidifiers.

The amount of moisture that can be carried by a pound of air increases rapidly with rise in temperature as shown in humidity charts. Therefore, for any given product, the highest temperature possible should be used because of faster drying and smaller requirements for ventilation. The limiting conditions

are those principally set by the properties of the product itself. From atmospheric data supplied by the Weather Bureau of Cambodia, it seemed likely that it would be possible to employ air temperatures considerably higher than those normally used for the artificial drying of Atlantic salt codfish in Canada. Therefore the prospects appeared hopeful for a satisfactory drying rate even in the absence of a dehumidifying system. This working hypothesis was based on the theoretical considerations outlined hereunder.

With wet fish the drying rate depends mainly on the difference in temperature between the air stream and the wet surface of the fish, which assumes a temperature corresponding to the wet-bulb temperature of the air. When external dehumidification is applied, the absolute humidity is decreased and consequently the wet-bulb temperature is reduced. This increases the difference between the dry- and wet-bulb temperatures and the drying rate. However, we know from psychrometry that the difference between the dry- and wet-bulb temperatures will also increase with an increase in the temperature of the air, even though the absolute humidity remains constant. A thermocouple system of control, based on the latter principle, yielded interesting results with light and heavy salted codfish (Legendre, 1958). The method uses a thermocouple, inserted in the flesh near the surface, to regulate temperature of the air circulating in the dryer. There is no danger of overheating the product and the air is always at the highest possible temperature. Dehumidification is required only when it is known that the highest feasible dry-bulb temperature of the air does not produce a satisfactory drying rate.

Information concerning drying of Cambodian fish is scarce. Therefore it was decided to run a series of drying experiments here at Grande-Rivière, before making any attempt to design a dryer.

The Colombo Plan officers organized and executed the dispatch of semi-dried salt fish from Cambodia to Grande-Rivière.

The purpose of these experiments was to ascertain the highest temperature that may safely be employed and to determine the drying rate at this temperature. Having secured this information, the next step would consist of designing an appropriate apparatus, suitable for the preparation of dried Cambodian salt fish under the unfavourable atmospheric conditions prevailing in that country during the rainy season.

DRYING POSSIBILITIES OF CAMBODIAN FISH

GENERAL PROCEDURE

The fish sent from Cambodia by air arrived here after 2 weeks. They had been semi-dried and corresponded to the product which usually is sent to the central plant in Cambodia. The 2-week trip did not seem to affect the quality of the product. There was some odour of rancidity but apparently this is not always regarded as detrimental in some Cambodian-processed fish products.

The air shipments consisted of representatives of several species (Table I). Each was analyzed before and after drying. The drying experiments were performed with the already available experimental salt fish dryer designed at this Station. This dryer is of the batch compartment type and is equipped with temperature and relative humidity controllers so that any temperature between 60 and 150°F (15.6 and 66°C) and any relative humidity between 30 and 90% can be maintained.

The air circulating over the fish inside the dryer was maintained at a constant velocity of about 350 feet (107 m) per minute. During the drying experiments, samples were taken at intervals and weighed. The data recorded here represent the loss of moisture by the fish and the values refer to "dry basis" (pounds of moisture lost per 100 lb of bone-dry material). This value, represented by the symbol L and the drying rate $\Delta L/\Delta \theta$ (pounds of moisture lost per hour per 100 lb of dry material where θ = time in hours), is obtained directly by a simple graphical differentiation of the moisture-loss curve. Moisture determinations were made by the oven method using a temperature of 105°F (40.5°C). Salt content analyses were made by the silver nitrate method (Dyer, 1943). The fat content was determined by Soxhlet extractions with ether.

DRYING EXPERIMENTS

The results of the first series of experiments indicated clearly that it is possible to dry fish artificially. No difficulties were experienced. The analytical figures, shown in Table I, were obtained before and after drying at 80, 90 and 100°F and at relative humidities of 40, 50 and 60%. Equally good products were obtained in all experiments. As expected, the best drying rates were observed at high temperatures and low relative humidities. The drying rate is higher than that of light salted codfish. This is probably due to the fact that the Cambodian fish is smaller and thinner, and also because it is cut and split in such a way as to increase the exposed surface or to decrease the actual thickness

TABLE I. Results of analysis made on the first shipment of Cambodian fish.

	Name of fish					
	Trey Chhkok		Trey Chdor	Trey Pra	Trey Linh	Chhkok Tituy and Chhpin
	Large	Small				
	%	%	%	%	%	%
Fat content (dry basis)	1.25	16.1	5.7	12.7	29.5	22.3
Salt content (dry basis)	33.0	21.0	28.6	29.7	17.9	14.7
Moisture content (wet basis)	50.0	40.0	40.0	42.0	31.4	39.2
Moisture content (wet basis) after 24-hour drying period at:						
Temp. 80°F (26.7°C), Relative humidity 60%	40.5	24.6	32.1	34.3	20.5	28.6
Temp. 90°F (32.2°C), Relative humidity 50%	36.3	18.9	29.3	32.1	18.1	27.7
Temp. 100°F (37.8°C), Relative humidity 40%	32.6	13.6	24.1	21.2	13.5	17.7

of the fish. The fat content of most of these fish is much higher than that of cod-fish. Only two products, namely Trey Chdor and large Trey Chhkok, were found to have a low fat content (Table I). According to their salt content the samples may be classified as light and medium salted fish.

As the initial moisture content of the batches of fish used in the first experiments was quite low it was considered desirable to repeat the experiments with other batches of higher moisture content.

The initial water content of the second batch of Trey Chdor and Trey Linh was about 10% higher than in the first batch (Table II). Correspondingly the quality was not as high on arrival. The product was softer and the smell of rancidity was stronger than with the first batch. It was found also that the fat content of the Trey Chhkok samples (large and small) was much higher than in the first shipment. In spite of these detrimental factors good results were

TABLE II. Results of analysis made on the second shipment of Cambodian fish.

	Name of fish			
	Trey Chhkok		Trey Chdor	Trey Linh
	Large	Small		
	%	%	%	%
Fat content (dry basis)	14.2	33.5	2.5	27.4
Salt content (dry basis)	25.7	20.1	24.5	28.8
Moisture content (wet basis)	50.4	40.0	56.5	41.8
Moisture content (wet basis) after 30-hour drying period at:				
Temp. 80°F (26.7°C), Relative humidity 30%	35.5	20.0	35.0	..
Temp. 80°F (26.7°C) Relative humidity 50%	36.0	23.9	40.6	...
Temp. 100°F (37.8°C) Relative humidity 50%	37.5	20.6	39.2	...
Temp. 110°F (43.3°C) Relative humidity 50%	...	23.8	35.8	11.0

obtained with all samples, even when drying temperatures as high as 110°F (43°C) were used.

In judging the quality of the Cambodian products, the author applied his experience with Canadian salt cod and considered the general appearance only. Since this judgment is not necessarily compatible with the requirements and food habits of Cambodia, confirmation of his views was requested from Mr Bérubé and visitors from Indonesia. According to these referees, the quality of the artificially dried products was decidedly satisfactory and comparable to a good average quality product marketed in Cambodia. It was therefore concluded that a temperature of 110°F is not harmful for these products and can safely be used to dry Cambodian fish artificially. If we consider that an increase in

temperature results in a decrease in relative humidity and consequently increases the drying potential of the air, it is warrantably concluded that, taking into account the atmospheric conditions in Cambodia, a temperature of 110°F will result in a relative humidity low enough to permit drying without any special dehumidifying system.

VARIATIONS OF DRYING RATE

From the weighings made during the drying experiments the moisture-loss curves were constructed. From these the drying-rate curves were obtained by graphical differentiation. Figure 1 shows the moisture-loss and drying-rate

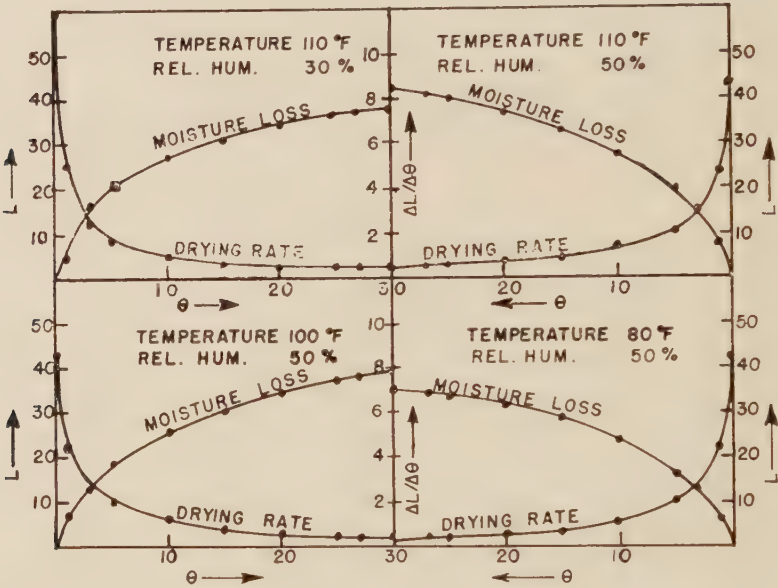


FIG. 1. Moisture loss and drying rate curves obtained with Cambodian fish—Trey Chhkok. (L = moisture loss in pounds per 100 pounds of dry material; $\Delta L / \Delta \theta$ = drying rate in pounds per hour per 100 pounds of dry material; θ = time in hours.)

curves obtained with Trey Chhkok at various temperatures and relative humidities. Figure 2 shows the corresponding curves obtained with Trey Chdor. Both these series of curves were obtained with the second batch of fish. The corresponding data are shown in Table III and indicate that the drying rate is much higher with Trey Chdor than with Trey Chhkok. However, the variations of the drying rate, which are caused by changes in temperature or relative humidity, are about the same in both cases. As expected, the drying rate increases with temperature and the increase is encountered during the whole drying operation. Therefore, the overall moisture loss is much higher at a

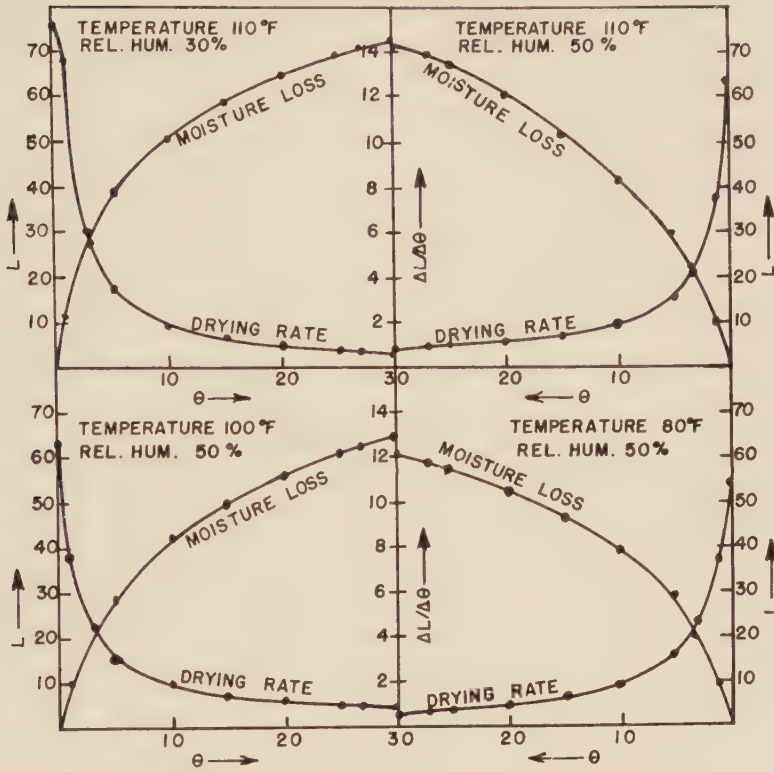


FIG. 2. Moisture loss and drying rate curves obtained with Cambodian fish—Trey Chdor. (L = moisture loss in pounds per 100 pounds of dry material; $\Delta L/\Delta \theta$ = drying rate in pounds per hour per 100 pounds of dry material; θ = time in hours.)

high temperature than at a lower temperature. From these experiments 110°F (43°C) seems the best temperature to be used for the artificial drying of Cambodian fish. Higher temperatures could not be studied with the limited amount of material on hand but it is not impossible that they could be used.

The relative humidity influences the drying rate mainly during the first part of the drying operation, when the surface is wet or partly wet. For example, with Trey Chhkok the drying rate during the first two drying hours is higher at 30% relative humidity than at 50%. Near the end of the operation however, when case-hardening occurs, the picture is reversed. The overall result is that the total moisture loss is slightly higher at 50% than at 30%. A similar effect was encountered with Trey Chdor, but in that case the total moisture loss was about identical for both relative humidities. To avoid case-hardening it would be necessary to use a low relative humidity at the beginning and to increase it for the last part of the operation. This procedure was successfully applied to Gaspé-cure fish (Legendre, 1955). Another way could be to use thermocouple

control (Legendre, 1958). If the relative humidity is to be kept constant for the complete operation from beginning to end, it should be regulated to around 50 to 55%.

In all experiments an air velocity of 350 feet (107 m) per minute was used. It is well known that high air velocities increase the amount of heat transferred between the air and the product, as compared with lower air velocities, so that the drying rate increases. Besides, high air velocities usually result in more uniform conditions inside the dryer. However, the horsepower requirements increase very rapidly with increasing air velocities and it is generally considered more economical to use an air velocity ranging from 250 to 500 feet (76 to 152 m) per minute, which results in a satisfactory drying rate, adequate air distribution and heat transfer.

ATMOSPHERIC CONDITIONS

Readings of temperatures and relative humidities for different periods of the year 1954 were obtained from Cambodia and the averages of these readings are shown in Table IV. It may be seen that the mean dew points fluctuate between 72.5 and 77°F (22.5 and 25°C) during the dry and the humid months. This is explained by the fact that an increase in relative humidity corresponds to a certain decrease in temperature.

TABLE IV. Atmospheric conditions in Cambodia, 1954.

	Dry months		Humid months	
	March	April	August	September
Mean temperature, °F (°C)	85.3(29.5)	96.6(35.9)	83.1(28.4)	81.3(27.4)
Mean relative humidity, %	64.9	72.1	81.1	82.7
Mean dew point, °F (°C)	72.5(22.5)	77.0(25.0)	77.0(25.0)	75.5(24.2)

For practical purposes calculations were based on a dew point of 77°F (25°C). Assuming this value and 110°F (43°C) as the temperature of the air which will be used to circulate over the fish, it may be found from psychrometric charts that the resulting relative humidity will be about 36%. This is certainly low enough to permit good drying without additional dehumidification.

ARTIFICIAL DRYER FOR CAMBODIA

Since the results of the experiments reported above justify the establishment of an industrial dryer in Cambodia, it was decided to recommend one of 2-ton (1800-kg) capacity for the following reasons.

A unit of this size would be large enough for the Cambodian technicians to experiment on the preparation of batches on an industrial scale. Batches of 2 tons would also be representative enough for judging the quality obtained

according to local market requirements. Besides, types of fish other than those investigated and described in this paper could be dried experimentally, and finally this 2-ton dryer is designed in such a way that four or six similar sections could be added whenever necessary.

GENERAL ARRANGEMENT

Figure 3 shows a sketch of the experimental dryer for Cambodia. The dryer is very simple and consists essentially of a drying tunnel, a fan and a steam heater. It may be noted that no provision has been made for recirculating the air. In temperate regions recirculation is required on account of large variations in the dew points of the atmosphere. In Cambodia, however, the dew point does not vary extensively and for practical purposes the inlet conditions can be assumed to be constant if the temperature is regulated. Since the dew point is around 77°F (25°C) the inlet air is constantly moist and the outlet air after passing over the fish has therefore a higher moisture content. Recirculation

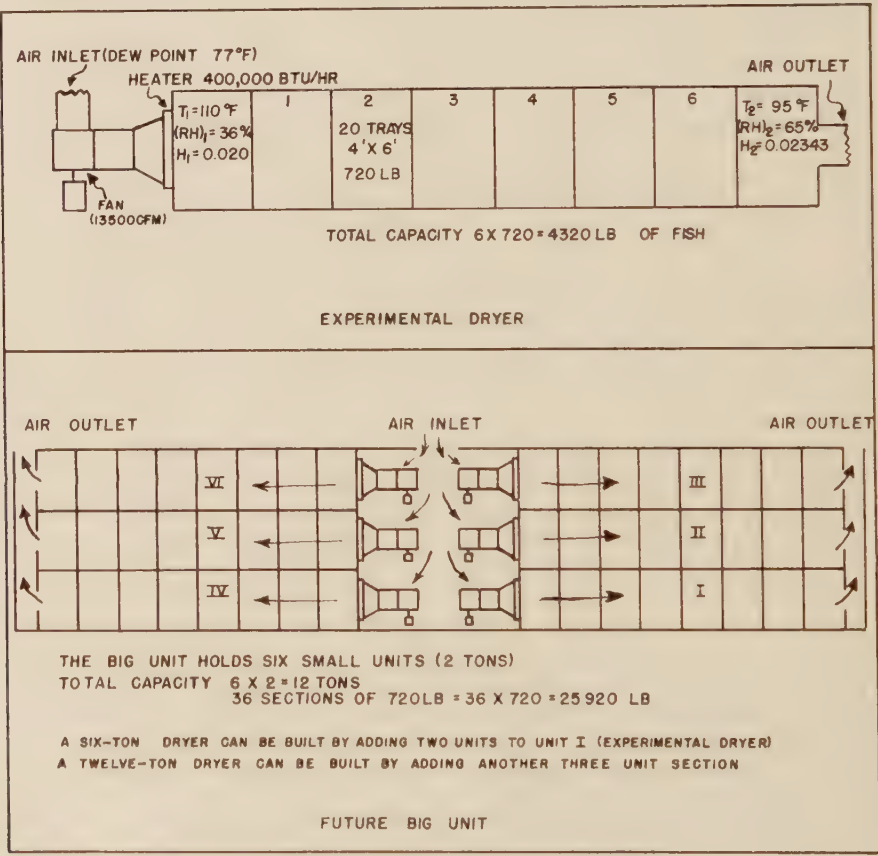


FIG. 3. Sketch of dryer for Cambodian fish.

would thus reduce the efficiency of the dryer. The only control equipment is a temperature controller which is set at 110°F (43°C) and which should be located at the beginning of the drying tunnel. The mean relative humidity of the air in the dryer depends on the inlet conditions and on the amount of moisture removed from the fish. It will therefore vary with the overall drying rate. In a following section of this paper detailed instructions are given for a procedure which will give a more uniform overall drying rate and consequently a more constant relative humidity.

NUMBER OF TRAYS

A dryer of a 2-ton capacity suitably consists of six sections, holding about 700 lb each. It was found experimentally that 1.5 lb of fish required about 1 square foot on the trays. The usual size of the trays being 4 by 6 feet, each will then hold about $4 \times 6 \times 1.5 = 36$ lb of fish. Using 20 trays per section, or $20 \times 36 = 720$ lb of fish, this will give a total capacity of $6 \times 720 = 4320$ lb of fish in the dryer. The distance measured from centre to centre of the different trays should be 4 inches; therefore the inside height of the dryer will be $(21 \times 4)/12 = 7$ feet.

INLET AND OUTLET CONDITIONS

It was explained above that the dew point in Cambodia may be assumed as 77°F and that an inlet temperature T_1 of 110°F will result in a relative humidity $(RH)_1$ of 36%. Psychrometric charts show that under these conditions the absolute humidity of the air H_1 is 0.02000 lb of water per pound of dry air. It was shown also that the relative humidity of the air will vary with the overall drying rate. Therefore, the best design for a dryer should combine the highest possible relative humidity with the maximum drying rate. It is however not practical to use relative humidities higher than 65% because above this percentage the drying rate is reduced considerably. Psychrometric data show that a Cambodian dryer designed to work at a relative humidity $(RH)_2$ of 65% at the outlet will have an outlet temperature T_2 of 95°F and that its absolute humidity H_2 will be 0.02343 lb of water per pound of dry air. This is valid under the assumption that all the sensible heat given by the air is used to evaporate water from the fish inside the dryer. Consequently, the weight of water gained by each pound of dry air is equal to:

$$H_2 - H_1 = 0.02343 - 0.02000 = 0.00343 \text{ lb water/lb dry air.}$$

AIR REQUIREMENTS

The highest drying rate equal to 10 lb of water/hour/100 lb of dry material is encountered at the beginning of the drying operation when the moisture content of fish (Trey Chdor) is around 56.5% (Table II). Since the total capacity

of the dryer is equal to 4320 lb the overall weight of moisture taken from the fish by the air will be:

$$\frac{4320 \times 0.435 \times 10}{100} = 188 \text{ lb/hr.}$$

It was found above that each pound of air will gain 0.00343 lb of water. The air required is then equal to:

$$\frac{188}{0.00343} = 54800 \text{ lb/hr.}$$

The mean specific volume of the air inside the dryer (100°F and 50% R.H.) is found to be 14.6 cu ft/lb. Therefore, the volume of air circulating over the fish will be:

$$\frac{54800 \times 14.6}{60} = 13300 \text{ cu ft/min.}$$

For a free area of about $6 \times [7 - (20 \times 0.1)] = 6 \times 5 = 30$ sq ft the velocity of the air in the dryer will be:

$$\frac{13300}{30} = 444 \text{ (} = \text{approximately 450) ft/min}$$

The mean specific volume of the ambient air in Cambodia (dew point = 77°F as assumed before) is found to be 14.26 cu ft/lb. Therefore, the required volume of air entering the dryer will be:

$$\frac{54800 \times 14.26}{60} = 13020 \text{ (} = \text{approximately 13000) cu ft/min.}$$

HEAT REQUIREMENTS

Before entering the dryer, the air will have to be heated from about 80°F to 110°F (T_1). For an absolute H_1 of 0.020 the humid heat of the air is equal to:

$$0.24 + (0.446 \times 0.020) = 0.24 + 0.00892 = 0.249 \text{ BTU/lb/°F.}$$

Therefore the total heat requirement will be:

$$54800 \times 0.249 \times (110 - 80) = 410,000 \text{ BTU/hr.}$$

STEAM HEATER AND SUPPLY FAN

We know that 13000 cu ft/min of air at 80°F will have to be heated to 110°F by a steam coil. For this, a boiler having a capacity large enough to furnish about 410,000 BTU/hr to the steam heater is required. The pressure of the steam in the coil may be chosen to be around 5 lb. If we assume for the air circulating through the heater a face velocity of about 800 ft/min the required face area for the coil will be 16 sq ft. Therefore, a section of 4×4 ft may be chosen.

The resistance to air flow through the steam heater depends on various factors of which the face velocity of the air is certainly the most important. It

may be found from various tables of performance data that the air friction through the required coil will be around 1/6 or 0.167 in of water.

The resistance of air flow through the dryer may be found by assuming a clearance of 3 in between the dryer shelves and taking the formula for parallel plates for each of the 21 spaces.

$$\text{Then: } p = \frac{12\mu LU}{ga^2} \text{ (Walker } et al., 1927)$$

where: p = pressure drop in lb/sq ft,

$$\begin{aligned} \mu &= \text{absolute viscosity of air (at } 80^\circ\text{F) in lb/sec/ft,} \\ &= 0.018 \times 0.000672 = 12.1 \times 10^{-6}, \end{aligned}$$

$$\begin{aligned} L &= \text{frictional length in feet} \\ &= 6 \times 4 = 24 \text{ ft (6 sections, 4-ft trays),} \end{aligned}$$

$$\begin{aligned} U &= \text{air velocity inside the dryer in ft/sec} \\ &= 450/60 = 7.5, \end{aligned}$$

$$g = 32 \text{ ft/sec/sec,}$$

$$\begin{aligned} a &= \text{Clearance between shelves in feet} \\ &= 3/12 = 0.25, \end{aligned}$$

$$a^2 = (0.25)^2 = 0.0625 \text{ sq ft.}$$

$$\begin{aligned} \text{Then: } p &= \frac{12 \times 12.1 \times 10^{-6} \times 24 \times 7.5}{32 \times 0.0625} \\ &= \frac{1.2 \times 1.21 \times 2.4 \times 7.5 \times 10^{-2}}{3.2 \times 6.25} \\ &= \frac{0.013 \times 12 \times 21}{62.3} = 0.053 \text{ in of water.} \end{aligned}$$

The resistance to air flow through the steam heater and through the dryer is $0.167 + 0.053 = 0.220$ in of water. There will be also some resistance at the outlet of the dryer and consequently it can be assumed that the total resistance against which the fan must operate is about 0.25 in of water. Therefore, the fan required must be able to handle 13000 cu ft of air per minute against a static pressure of 0.25 in of water. The horsepower output of the fan will then be:

$$\text{Air horsepower} = \frac{QP}{6356}$$

$$\begin{aligned} \text{where: } Q &= \text{volume of air circulated in cu ft/min} \\ &= 13000, \end{aligned}$$

$$\begin{aligned} P &= \text{static pressure in inches of water} \\ &= 0.25. \end{aligned}$$

$$\text{Then: Air horsepower} = \frac{13000 \times 0.25}{6356} = 0.51.$$

The horsepower input will be:

$$\text{hp} = \frac{\text{horsepower output}}{\text{efficiency}}.$$

Assuming an efficiency of 60% for the fan, then:

$$\text{hp} = \frac{0.51 \times 100}{60} = 0.85;$$

consequently, a 1-hp motor will be required for the fan.

OPERATION OF DRYER

The experimental dryer was designed in such a way that the cost of both operation and production is reduced to the minimum. The data shown in Fig. 3 are those obtained from the above calculations and apply to the highest drying rate which is encountered at the beginning of the drying procedure when a batch operation is being used. In that case the relative humidity at the end will never exceed 65% and will decrease when the drying rate is reduced. As shown in Fig. 1 and 2, the drying rate decreases very rapidly and after only 5 hours it is close to 3 lb water/hour/100 lb of dry material (Table III). At that stage the outlet conditions will be $T_2 = 105^\circ\text{F}$ and $(RH)_2 = 44.5\%$. Near the end of the operation when the value of the rate is about 1.0, the outlet conditions will be $T_2 = 108^\circ\text{F}$ and $(RH)_2 = 39\%$.

It is quite possible to construct other dryers which would have a better drying rate. However, for the design described here economy and ease of operation were the dominant considerations. These factors are certainly most important for this particular application. It is felt that the arrangement, if operated properly, will yield a product of satisfactory quality. As pointed out previously for the preparation of this and other types of dried fish the best possible drying rate is obtained when a low relative humidity is used for the first few hours (when the surface of the product is wet or partly wet) and a higher relative humidity for the later stages of the operation (when the surface is dry). With a simple batch operation as suggested here, the above cannot be applied. The relative humidity inside the dryer, which depends on the drying rate, will be high at the beginning and low at the end of the operation.

This complication can nevertheless be alleviated if the dryer is charged at regular intervals with smaller batches of one-quarter, one-third, or even one-half of its total capacity. That is to say, every time a quantity of green fish is charged, a similar quantity of dried fish is removed. Consequently the proportion of green, dried and semi-dried fish in the dryer will approach constancy throughout the process, variations of relative humidity will be reduced considerably, and the overall drying rate will be more uniform than in a true batch operation. To be more specific: the length of the dryer and the amount of newly charged fish determine the increase in relative humidity which in turn causes a reduction of the drying rate. But in the semi-continuous process outlined above the amount of newly charged fish is limited and therefore the increase in relative

humidity is minimized in comparison to a true batch operation. The presence of semi-dried fish is another favourable factor.

An additional improvement would be to use easily movable trucks carrying the trays and to feed the dryer at regular intervals as explained before. In that case the trucks carrying green fish should always enter the first section and be pushed gradually toward the last section inside the dryer, so that the properly dried fish is taken out from the last section. Such a procedure will result in a lower relative humidity for the green fish and in a higher relative humidity for the nearly dried product.

If the relative humidity of the air leaving the dryer falls too low, e.g. to between 40 and 50%, the use of a lower temperature for T_1 will correct the situation. For example a temperature of 100°F could be used during unusually dry months. On the other hand, if the relative humidity is too high some improvements are also possible. Several possibilities exist. If the relative humidity at the inlet $(RH)_1$ is high as well as at the outlet $(RH)_2$, the dew point of the air will be unusually high and the only way to correct the situation will be to try a higher temperature for T_1 . Good results were obtained at 110°F. Higher temperatures could not be investigated with the amount of fish available, but it is possible that they could be used successfully. If, however $(RH)_2$ is high but $(RH)_1$ is low enough, then the drying rate of the fish inside the dryer will be much higher than expected. This is not likely to happen, unless the dryer is filled with very wet fish. In this case, one of the procedures outlined above for loading the dryer will result in considerable improvements.

BIG DRYING UNIT

Figure 3 shows also the sketch of a proposed future big unit which comprises six small units similar to the one described above. The capacity of the big unit would be $6 \times 2 = 12$ tons or $6 \times 6 = 36$ sections of 720 lb each; $36 \times 720 = 25920$ lb capacity for fish. Movable trucks holding 20 trays (4×6 ft) were planned for each section and no partitions inside will be necessary because the sides of trucks allow adequate separation.

CONCLUSIONS

The results of drying experiments conducted with Cambodian fish show that they can be dried artificially without any difficulty. A good drying rate was obtained because the product is cut and split in such a way as to provide large exposed surfaces.

A product which was judged as first-class quality was obtained with a drying temperature as high as 110°F (43°C). Because the dew point in Cambodia is always between 72.5 and 77°F (22.5 and 25°C), artificial drying without dehumidification is considered to be possible there, provided a temperature of 110°F is used.

ACKNOWLEDGMENTS

The author expresses his sincere thanks to Mr L. Bérubé, Officer of the Colombo Plan, who gave most valuable and detailed information on the situation in Cambodia and who made the arrangements for samples of Cambodian fish to be sent to Canada.

The technical assistance of Mr G. H. Imbeault, especially in conducting the determinations during the experiments, is also gratefully acknowledged.

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Probable Effects of Proposed Passamaquoddy Power Project on Oceanographic Conditions^{1, 2}

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ABSTRACT

The proposed Passamaquoddy power project involves the construction of a series of dams across the mouth of Passamaquoddy and Cobscook Bays. Passamaquoddy Bay, the proposed high pool, will be filled near high water by 90 filling gates, and Cobscook Bay, the proposed low pool, will be emptied near low water by 70 emptying gates. Water will flow continuously from the high pool to the low pool, through a 30-turbine powerhouse. Tidal range will be reduced to approximately 4 and 8 ft in the high and low pools respectively. The effect of this proposed installation on oceanographic conditions in the region has been considered. It is concluded that currents, within the impounded bays and in the area lying inside the Bliss Island-Head Harbour region, will be altered markedly. In the outer Quoddy Region, tidal stream directions will be altered only slightly, while the changes in speed will probably not exceed 20% of their present value. No significant change in residual flow is expected outside the Quoddy Region. Not more than a 1% increase in tidal range is anticipated for the entire Bay of Fundy. Inside the impounded bays, there will be increased stratification. Seasonal variations in temperature of the surface layer will be increased. The summer maximum is expected to reach 20°C and the winter minimum will be less than 0°C. Ice cover is expected to occur over part of the impounded waters. Salinities at the surface will be reduced. Only minor changes in temperature and salinity of the deep layer are anticipated. No significant changes are expected in temperature or salinity in the outer Quoddy Region.

INTRODUCTION

THE ENERGY involved in ocean tides is tremendous, and there has been much speculation upon methods by which useful power might be extracted for man's use. On a small scale, power has been developed by tide-mills in Europe, England and America for several centuries. In recent years serious consideration has been given to large-scale harnessing of the tides, and at the present time a project for the development of tidal power is under way for La Rance River in France. Other schemes have been proposed for the Severn River in England, San Jose in Argentina, Mont St. Michel in France, and portions of the Bay of Fundy in Canada and the United States.

The Bay of Fundy is well known for the extreme tidal range which exceeds 50 ft near its head. This single factor has made it one of particular interest to oceanographers and engineers. The tides of coastal embayments, in general, derive their energy from ocean tides rather than from direct action of lunar and solar gravitational forces. The extreme ranges produced in the Bay of Fundy are attributed to the fact that it has a configuration and physical dimensions

¹Received for publication December 1, 1960.

²International Passamaquoddy Fisheries Board, 1956-59. Scientific Report No. 31.

appropriate to make it a quarter-wave resonator with a period corresponding closely to the period of the semi-diurnal tidal component. This, combined with the narrowing and shallowing in its inner portion, gives rise to a tidal range that increases from approximately 9 ft near its entrance in the Gulf of Maine to greater than 50 ft at its head.

In considering the extraction of power from a tidal system it is wise to consider the probable effects upon the system itself. These effects in many instances are local only. The possibility of widespread effects, however, should not be overlooked in a system which owes many of its characteristics to a resonance phenomenon.

The first serious consideration of a tidal power development involving Passamaquoddy and Cobscook Bays was proposed by a hydraulic engineer, Dexter P. Cooper, in the early 1920's. Studies of the effects that dams in the Passamaquoddy area might have on the oceanography and fisheries of the region were conducted during the late 1920's and early 1930's. In part, the conclusions drawn from these studies (North American Council on Fishery Investigations, Proceedings 1931-1933, No. 2, 1935, p. 6) were as follows:

"The physical effects of the present mixing mechanism appear to be local and although the construction of the dams would influence the hydrographic conditions in the passages, it is not expected that their influence would extend far into or beyond the outer Quoddy Region.

"The influence of this local mixing on the supply of nutrient salts in the surface layers, where they are available for plant production, is almost entirely confined to the Quoddy Region. The conditions existing over the greater part of the Bay of Fundy appear to result from other factors, which would not be influenced by the dams. It is not considered that the construction of the dams would have an appreciable effect upon the production of plant life outside the Quoddy Region."

In 1956 the governments of Canada and the United States of America referred the problems involved with the Passamaquoddy power project to the International Joint Commission. In turn, the Commission established an Engineering Board and a Fisheries Board to study the problem and report on their findings. (Hart and McKernan, 1960).

In the present study of the Passamaquoddy power project, the basic arrangement proposed by the International Passamaquoddy Engineering Board is a two-pool plan (Fig. 1). It consists of a high pool filled at high tide, a low pool emptied at low tide, and, between the two pools, a powerhouse through which flow from the high pool to the low pool would generate continuous but fluctuating power. The plan involves the impounding of water in Passamaquoddy and Cobscook Bays which would be maintained as the high and low pools respectively.

The proposed physical conditions to be imposed on the area warranted, as a first step, an extensive study of the region to determine the present circulation, tides, distribution of properties, and the controlling or relating factors. The second step was to consider what changes might be expected if dams were installed.

Oceanographic data from the Passamaquoddy region gathered over a period of 50 years prior to 1957, together with extensive observations and measurements taken in 1957 and 1958, were used as a basis for predicting the new conditions that might result from the construction and operation of the power project.

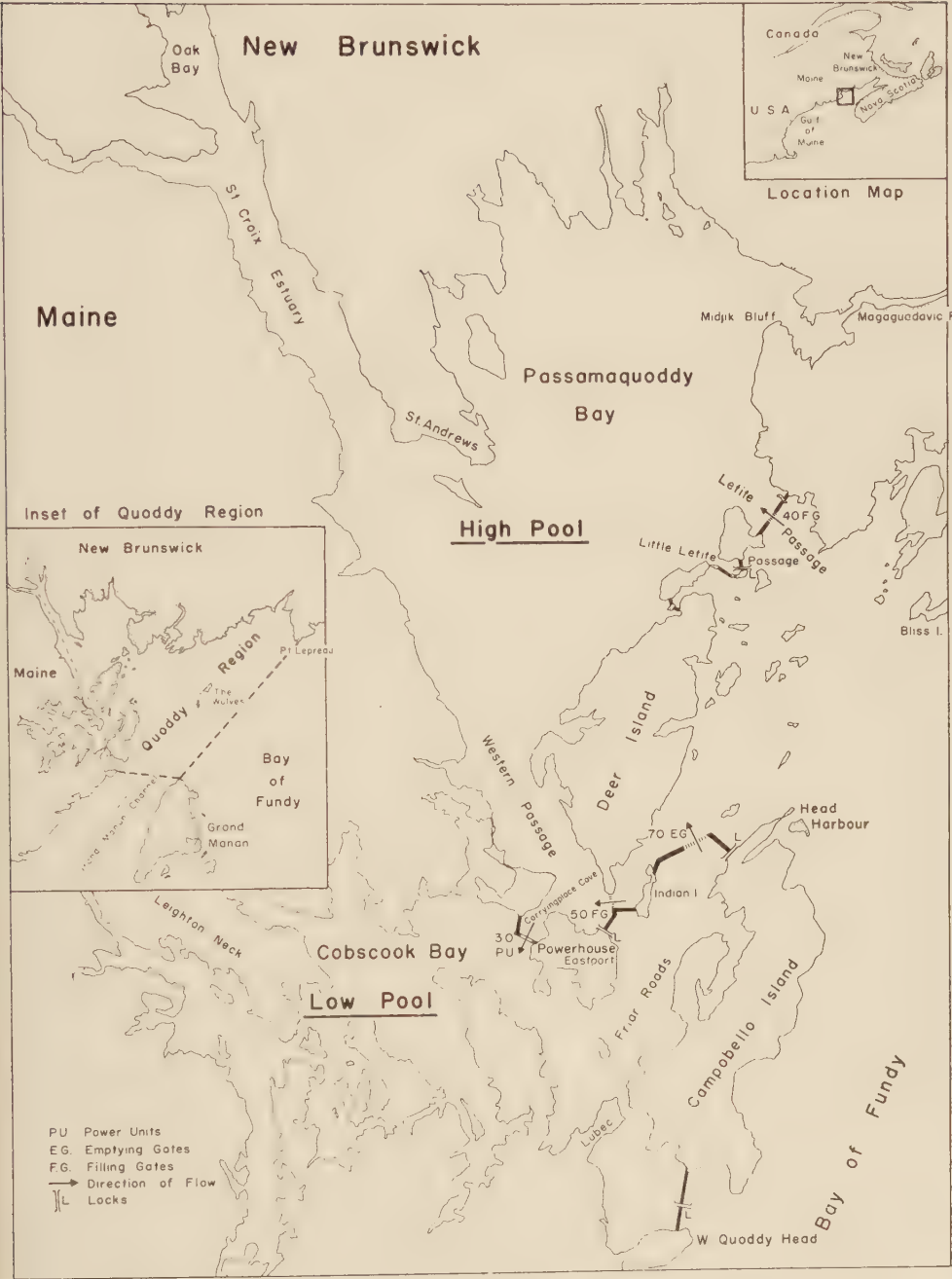


FIG. 1. Map showing location of high pool, low pool, filling gates and powerhouse. The Quoddy Region is shown in inset.

POWER PROJECT

This section deals with those engineering aspects of the power project that are involved in the changes that can be expected in the physical oceanography and the fisheries of the region. In some instances, the material included is in the form obtained from the Passamaquoddy Engineering Board. In other cases, computations from the basic data supplied by the engineers were necessary in order for the material to be in the form required by the Passamaquoddy Fisheries Board.

PROJECT LAYOUT

The final project arrangement selected for detailed design includes approximately 70 sq mi (square nautical miles) of Passamaquoddy Bay as the high pool, and 30 sq mi of Cobscook Bay and Friar Roads as the low pool, with a powerhouse located at Carryingplace Cove (Fig. 1). The plan calls for 90 filling gates, 40 in Letite Passage and 50 in Western Passage. The filling and emptying gates, which are of the same design (Fig. 2-A), are each 30 by 30 ft with a vertical lift set in a venturi throat and placed side by side. The venturi throat permits maximum velocity head and discharge rate for a given gate area. The total length of the filling gates structure in Letite Passage is 1440 ft and in Western Passage, 1800 ft (Fig. 3). The elevations, with reference to mean sea level, of the top and the bottom of the throat of the gates are -10 and -40 ft respectively. The maximum change in pressure in going through the gates would amount to about 4 lb/in².

It is planned to install 70 emptying gates between Pope Island and Green Island, occupying a total length of 2520 ft (Fig. 3). The top and the bottom of the throat of the emptying gates are at elevations of -23 and -53 ft respectively.

The minimum cross-sectional area in the flow occurs in the throat, which is 900 ft² per gate. The cross-sectional area increases rapidly upstream from the throat, but only slowly in the downstream direction. Velocities are inversely proportional to cross-sectional areas and are given (Fig. 2-B) as ratios of velocity at any point to the throat velocity. Maximum speeds will exceed 24 ft/sec during spring tides. Under maximum flow conditions, the time required to pass completely through the gate structure (110 ft) would be about 6 sec. Where necessary, excavation will be made to a depth of 45 ft on either side of the filling gates, and to approximately 55 ft on either side of the emptying gates.

The Carryingplace Cove powerhouse is planned to consist of 30 turbines rated at 10,000 kw each, placed side by side, occupying a total length of 2400 ft. There will be a channel excavated in the forebay of the powerhouse to connect with the high pool (Fig. 1). It will vary in depth from 33 to 50 ft and in width from 1800 to 2400 ft. Velocities in the channel are expected to be approximately 3 ft/sec.

The plans call for a total of four navigation locks. Two small locks, one in Little Letite Passage and the other near West Quoddy Head, to be 100 by 25 by

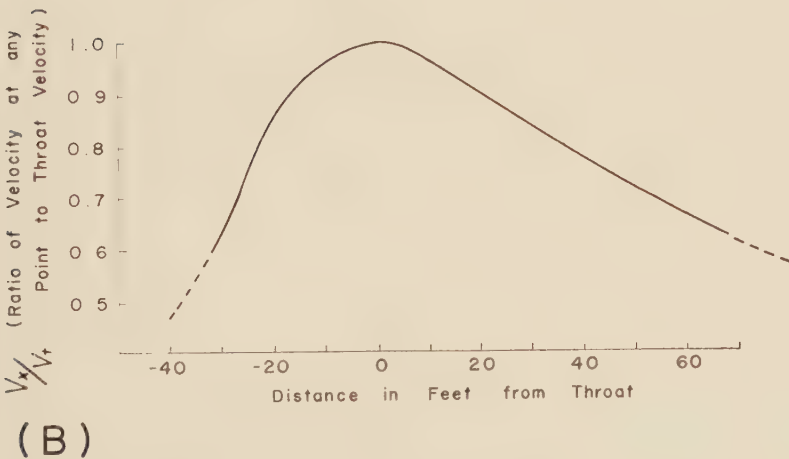
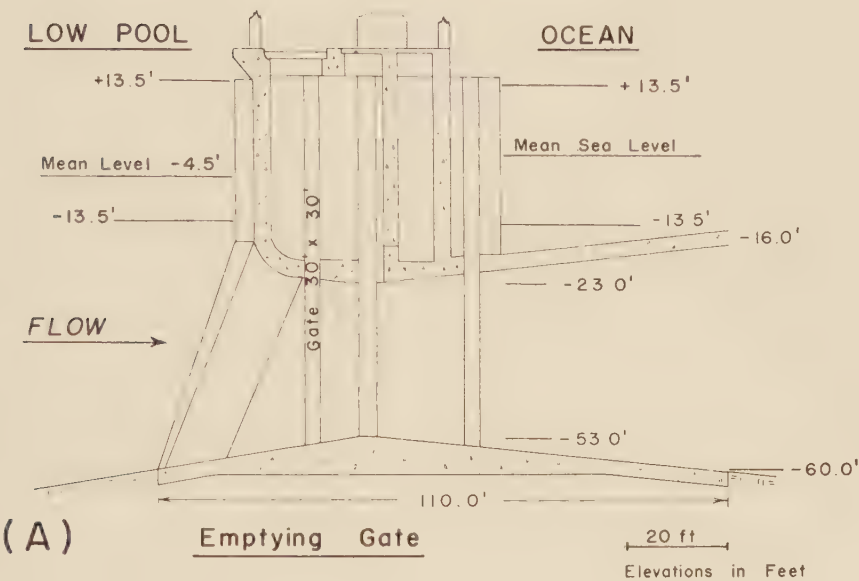


FIG. 2. (A) Cross-section of an emptying gate and (B) ratio of velocity at any point to throat velocity of gate.

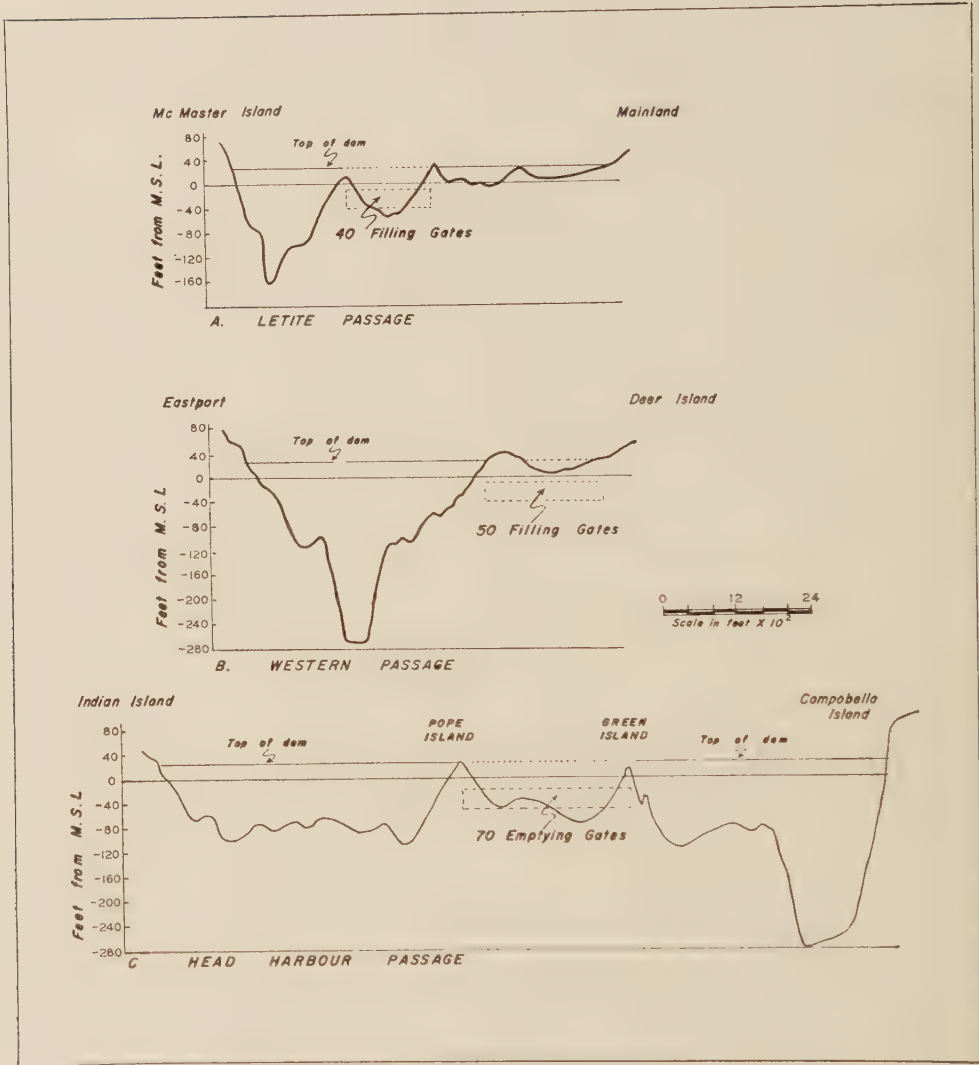


FIG. 3. Cross-sections in Letite, Western and Head Harbour Passages showing location of filling and emptying gates.

10 ft, are designed for small vessels (Fig. 1). Two large locks, one near Wilsons Beach and the other at Eastport, of dimensions 400 by 60 by 21 ft each, are designed to permit access of large vessels to both the low and high pools.

CYCLE OF OPERATIONS

The principle of operation is to maintain a hydraulic head between the high pool and the low pool. The high-pool filling gates will be opened only during times when the water level outside is higher than the level of the high pool. The emptying gates will be opened only when the level outside is lower than the level of the low pool. Water will flow continuously from the high pool through turbines to the low pool. The time variations in water level in the high pool, low pool and outside, are shown in Fig. 4. The sequence of events for a 12.4-hr cycle would be:

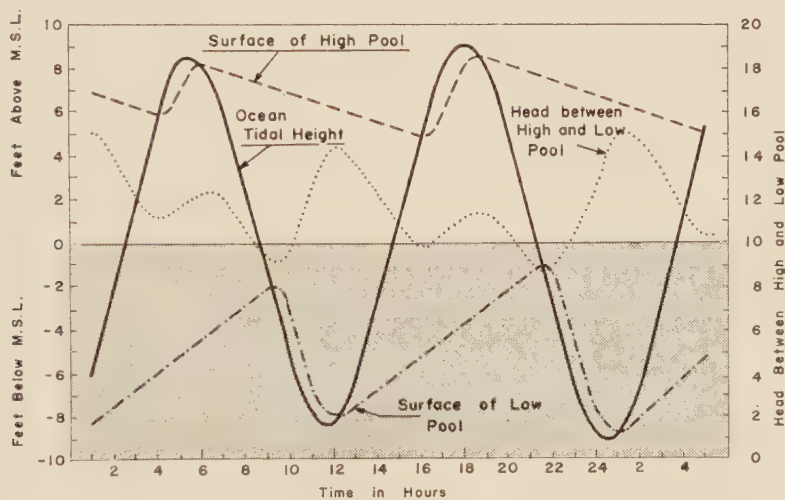


FIG. 4. Daily cycle of power project operation showing head between high and low pools, and the variation in water level for the high pool, low pool and outside areas.

1. The filling gates are closed soon after high water, when the inflow ceases and the level in the high pool is equal to the level outside. At this stage the high pool is at its greatest elevation.
2. Both filling and emptying gates remain closed (2.5-hr period) until the level outside falls to the level of the low pool at which time the emptying gates are opened. At this stage the low pool is at its maximum elevation.
3. The emptying gates are closed (3.4-hr period) soon after low water when the level of the low pool is the same as the level outside. At this point the low pool is at its minimum elevation.

4. Both filling and emptying gates remain closed (3.5-hr period) as the tide outside rises, until the elevation of the high pool and that outside become equal, when the filling gates are opened. At this point the high pool is at its minimum elevation.

5. The filling gates remain open (3.0-hr period) until conditions in paragraph 1 above exist, which completes the 12.4-hour cycle of operation.

WATER LEVELS AND FLOW CONDITIONS

In Fig. 5 the time variations in water levels are shown respectively for spring tide, mean tide and neap tide in the high pool, low pool and open ocean. The

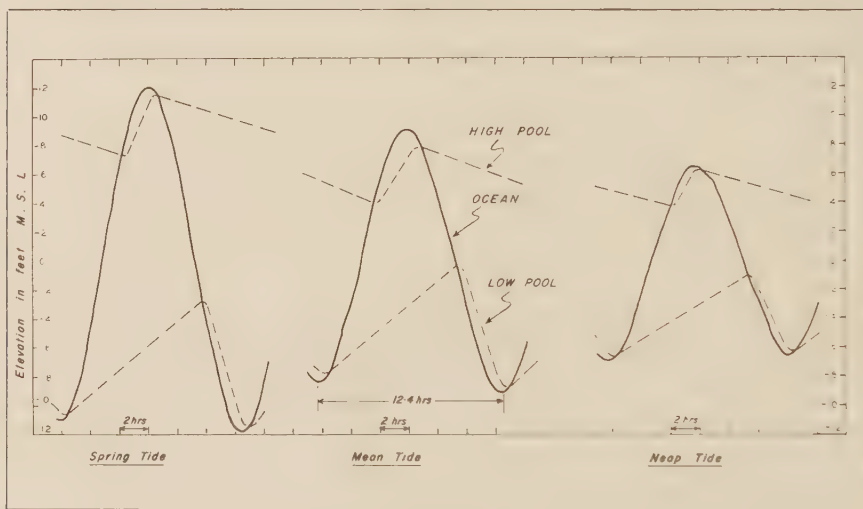


FIG. 5. Time variations in water levels in high pool, low pool and open ocean for spring, mean and neap tides.

open ocean tides shown are predicted ones for Eastport, Maine. For the spring tide the falling range is 24 ft. This range is exceeded in 1% of occurrences. For mean tide the falling range is 18.2 ft (exceeded in 45% of occurrences), and for neap tide the falling range is 13 ft (exceeded in 98.3% of occurrences).

Mean level will be raised in Passamaquoddy Bay about 6.4 ft and lowered in Cobscook Bay about 4.5 ft. The mean range in the high pool and the low pool will be 3.6 and 7.7 ft respectively.

During spring tides the average water level in the high pool will be raised 8.5 ft and will have a range of 4.4 ft. The maximum level reached in the high pool will be reduced 1.4 ft as compared to the level outside. The water level in the low pool will be lowered 6.2 ft and will have a range of 9.5 ft. At low water the level inside the low pool will be about 0.5 ft above the level outside.

During mean tides the average water level in the high pool will be raised 6.0 ft and will have a range of 3.9 ft. In the low pool the average water level will be lowered 4.0 ft and will have a range of 8.4 ft.

During neap tides the average water level in the high pool will be raised 4.6 ft and will have a range of 2.6 ft. In the low pool the average water level will be lowered 3.8 ft and will have a range of 5.3 ft.

In the high pool, the minimum elevation, which will occur during neap tides, and the maximum elevation, which will occur during spring tides, will be respectively 3.2 and 10.6 ft above the present mean sea level (Fig. 6).

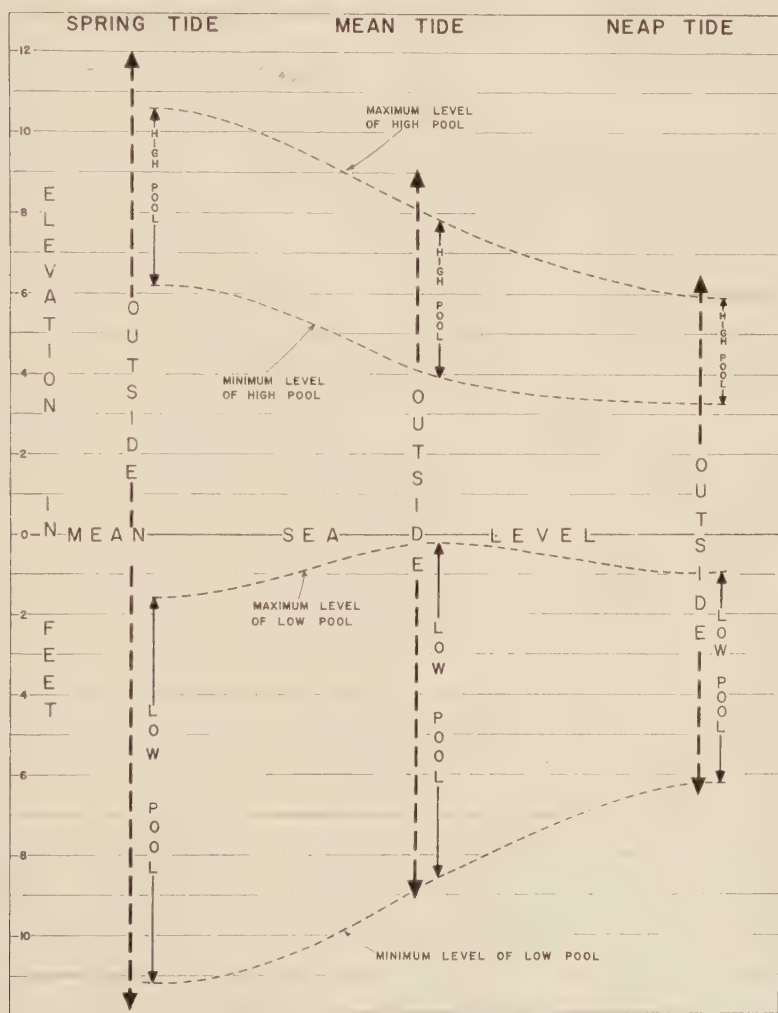


FIG. 6. Schematic illustration showing elevations and ranges of water levels in high pool, low pool and outside areas, for spring, mean and neap tides.

In the low pool the maximum elevation will occur during mean tides and the minimum elevation during spring tides. These will be respectively 0.0 and -11.4 ft relative to present mean sea level.

Flow through the filling gates, discharge through the turbines, and flow through the emptying gates, are shown in Fig. 7 for spring tide, mean tide and

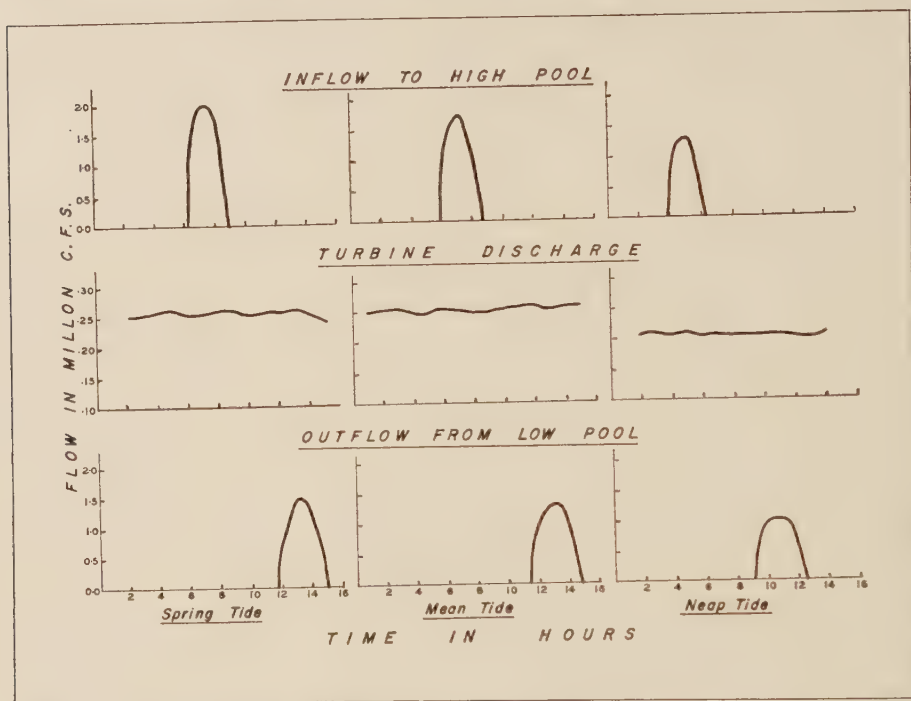


FIG. 7. Flow through the filling gates, discharge through the turbines and flow through the emptying gates.

neap tide. For comparison purposes, it should be noted that the inflow of fresh water to the high pool is, on the average, approximately 0.004×10^6 cfs (cubic feet per second) while the mean rate of flow through the passages filling Passamaquoddy Bay is 2.4×10^6 cfs.

The hydraulic head between the two pools will fluctuate during the cycle of operation between two maxima and two minima (Fig. 4). Maximum heads will occur at high tide and low tide while minimum heads will occur when the level outside is near mean sea level, on both the rising and falling tide. The head will fluctuate from a maximum during spring tides of nearly 20 ft to a minimum during neap tides of only 6 ft (Fig. 5). The average head will be approximately 12 ft. Flow through the powerhouse will average 0.285×10^6 cfs but will decrease to approximately 0.2×10^6 cfs for minimum flows.

POWERHOUSE

A cross-section of the Carryingplace Cove powerhouse through the center-line of one of its thirty 10,000-kw turbines is shown in Fig. 8. Each turbine has a vertical axis, fixed blades, a diameter of 320 inches, and turns at 40 rpm.

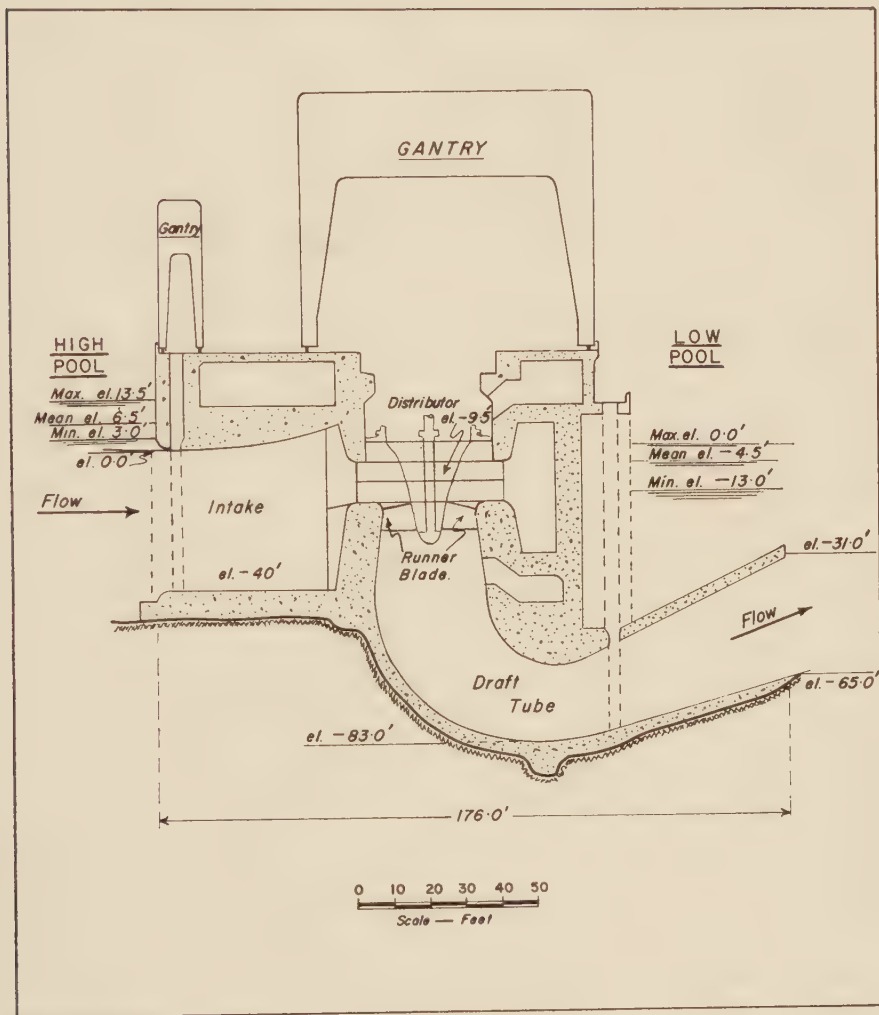


FIG. 8. Cross-section of powerhouse through centreline of turbine.

The cross-sectional area at the turbine intake is 40 by 65 ft. Mean velocity at this point is approximately 3 ft/sec. The top of the intake, which is at elevation zero, is 6.4 ft below the mean level of the high pool. A curve of the pressure along the centerline from intake to draft tube exit is shown (Fig. 9) for the case where the high pool is at elevation 6.4 ft, the low pool at elevation -4.5 ft, and

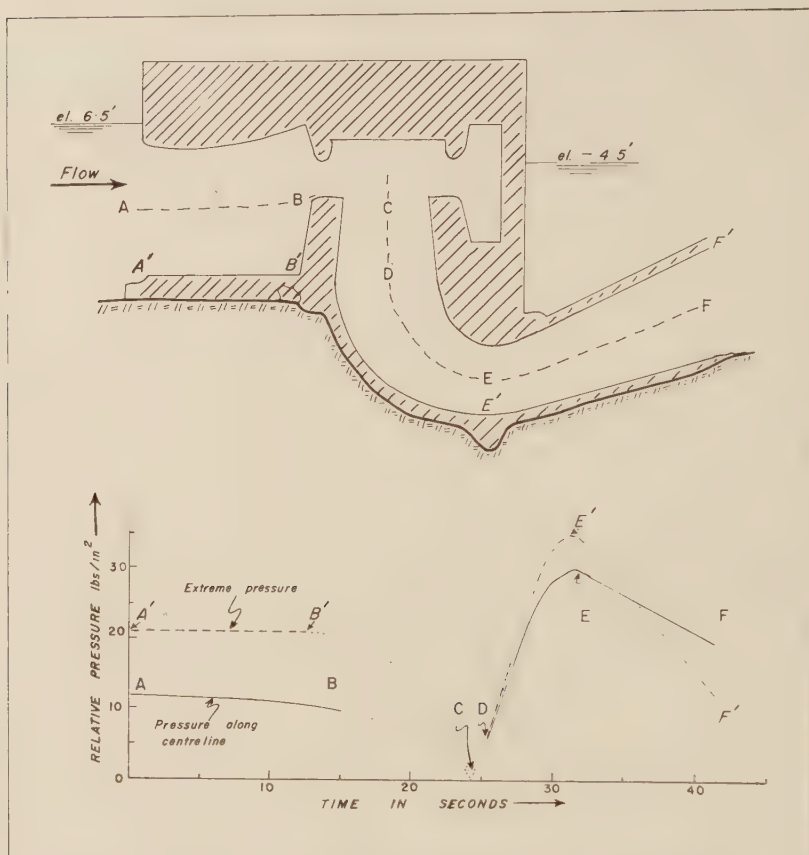


FIG. 9. Variation in pressure between intake and draft tube exit of powerhouse.

flow through the turbine is 0.285×10^6 cfs. Relative pressure varies from 13 lb/in^2 at the intake, to zero at the top of the draft tube, to 28 lb/in^2 at the bottom of the draft tube, to 19 lb/in^2 at the exit of the draft tube. The curve has been dotted in the region from the entrance to the distributors to the top of the draft tube, since adequate data to permit reliable calculations were not available. In order to indicate the most extreme conditions, a dashed curve has been constructed (Fig. 9) showing the approximate pressure that a fish would be subjected to if it passed in along the bottom of the intake, through the distributor and turbine to the bottom of the draft tube, finally leaving the powerhouse at the top of the draft tube. The most rapid pressure changes will occur between the distributors and the top portion of the draft tube, where pressure will change as rapidly as 7 $\text{lb}/\text{in}^2/\text{sec}$. Near the tips of the runner blades, the pressure will drop below atmospheric pressure and will approach the vapour pressure of water as the limit.

PRESENT CIRCULATION, TIDES AND DISTRIBUTION OF PROPERTIES

The oceanographic features of the Bay of Fundy are determined by the tide-producing forces, the earth's rotation, the fresh water discharged by the rivers, the meteorological conditions, and the bottom configuration. Of these factors, the tidal currents and amplitudes are dominant. Due to the strong tidal currents, which exceed 8 ft/sec in restricted areas (Forrester, 1960), vertical mixing of the water proceeds vigorously and hence seasonal fluctuations in temperature and salinity of the surface layer are much reduced.

One of the earliest systematic oceanographic surveys in the Bay of Fundy consisted of tidal current measurements by Dawson (1908). Since then, an extensive body of data has been collected, which has enabled a general description of the non-tidal circulation, and the spatial and temporal distribution of temperature and salinity. Copeland (1912), Craigie (1916), Vachon (1918), Hachey (1934c), Watson (1936), Hachey (MS, 1957) and Bailey (MS, 1957), have each dealt with certain aspects of Passamaquoddy Bay. Various studies of the oceanographic features of the Bay of Fundy have been published by Craigie and Chase (1918), Mavor (1922, 1923), Hachey (1934b), Watson (1936), Fish and Johnson (1937), McLellan (1951), MacGregor and McLellan (1952), Ketchum and Keen (1953) and Bailey *et al.* (1954). As a result of these studies, a comprehensive and valuable body of information is available concerning the gross features of temperature, salinity, circulation, and certain of the interrelationships and controlling factors have been established. Difficulty has been experienced, however, both in establishing with clarity the non-tidal circulation in the Quoddy Region (i.e., the area lying inside a line drawn from West Quoddy Head, Maine, to the northern tip of Grand Manan Island thence to Point Lepreau, N.B.), and in discovering any systematic relationship with the controlling factors. In order to provide a better understanding of the oceanographic features of the area, extensive field measurements were undertaken in 1957 and 1958. In the field program, direct current measurements were taken from an anchored ship at selected stations, temperature and salinity observations were made spatially and temporally throughout the region, electromotive force recorders were installed across some of the passages to determine transports, drift poles mounted with radar reflectors were tracked, and drift bottles were released at regular intervals throughout the area. In addition, surface samples were taken twice daily at the Biological Station wharf, St. Andrews, N.B. An anemometer was installed at Point Lepreau, N.B., and a tide gauge at the Government wharf at St. Andrews.

TIDES AND TIDAL CURRENTS

The remarkable tides in the Bay of Fundy have been attributed, in part, to the fact that the physical dimensions of the area are such that the natural period of vibration (quarter-wave) is approximately equal to the semi-diurnal tidal component.

The tide in a basin with one end closed and the other end in communication with the ocean is known as a co-oscillating tide. Fruitful results can be obtained

by considering the tides to be the resultant of a primary progressive wave and its reflected counterpart, with both undergoing damping due to frictional effects. Redfield (1950) made an analysis of the Bay of Fundy tides using the above approach and was able to relate the tidal range, time of high water, time of slack water, and phase difference of the primary and reflected waves throughout the bay for different coefficients of damping. In his conclusions, he suggested that "exceptional tidal ranges observed in such embayments as the Bay of Fundy are due to two or more stages in amplification by the combined effects of reflection and resonance in systems successively tributary to one another and to the ocean".

An investigation on the influence of the proposed tidal power project on the tides in the Bay of Fundy was carried out by Ippen and Harleman (MS, 1958). They approached the problem of describing the Bay of Fundy system in a manner similar to that of Redfield (1950) and then attempted to establish the relative "sensitivity" of the system to disturbances such as the proposed power project would involve. It is interesting to note that although two of the above-mentioned papers adopt a similar approach in describing the Bay of Fundy tidal system, the seaward end of the Bay of Fundy chosen for the analysis varies significantly. In Redfield's analysis, he considered the Bay of Fundy tidal system to conform satisfactorily to the theoretical expectation from the head of Chignecto Channel and the entrance to Minas Basin (where a point of reflection appears to be located) to a seaward point located in the vicinity of Lower East Pubnico in the southwestern part of Nova Scotia. The phase change undergone by the primary wave between these limits is about 80° . In the analysis made by Ippen and Harleman the seaward boundary was chosen at a point where the phase shift is only 68° and the amplification of the tide from ocean entrance to the head of the bay is two and one-half times. This compares to an amplification factor of approximately four in Redfield's analysis.

The net result of resonance combined with narrowing and shoaling in the inner reaches of the Bay of Fundy is that the tidal range increases from approximately 9 ft in the Gulf of Maine to greater than 50 ft at the head of Minas Basin. In the Quoddy Region the mean range of the tide varies from about 16 ft at West Quoddy Head to 20 ft near the head of the St. Croix estuary. The extremes vary from approximately 14 ft at neaps to a maximum of nearly 28 ft at springs. The mean range in the region is taken as 18 ft. Differences in the time of occurrence of high or low water throughout the Quoddy Region are less than an hour.

Tidal currents in most areas of the Bay of Fundy are nearly rectilinear, reversing direction approximately every 6 hr (Forrester, 1960). Speeds vary widely from place to place throughout the area, with currents in restricted passages, such as Letite, reaching a mean maximum value of 8 ft/sec. In Passamaquoddy Bay speeds are mostly less than 1 ft/sec. In Cobscook Bay mean maximum speeds near the mouth are approximately 5 ft/sec. In the region beyond the passages and bays (outer Quoddy Region) speeds seldom exceed 5 ft/sec. Speeds recorded were usually a maximum at the surface and decreased slowly with depth. In Fig. 10 and 11, the tidal streams at the surface are shown

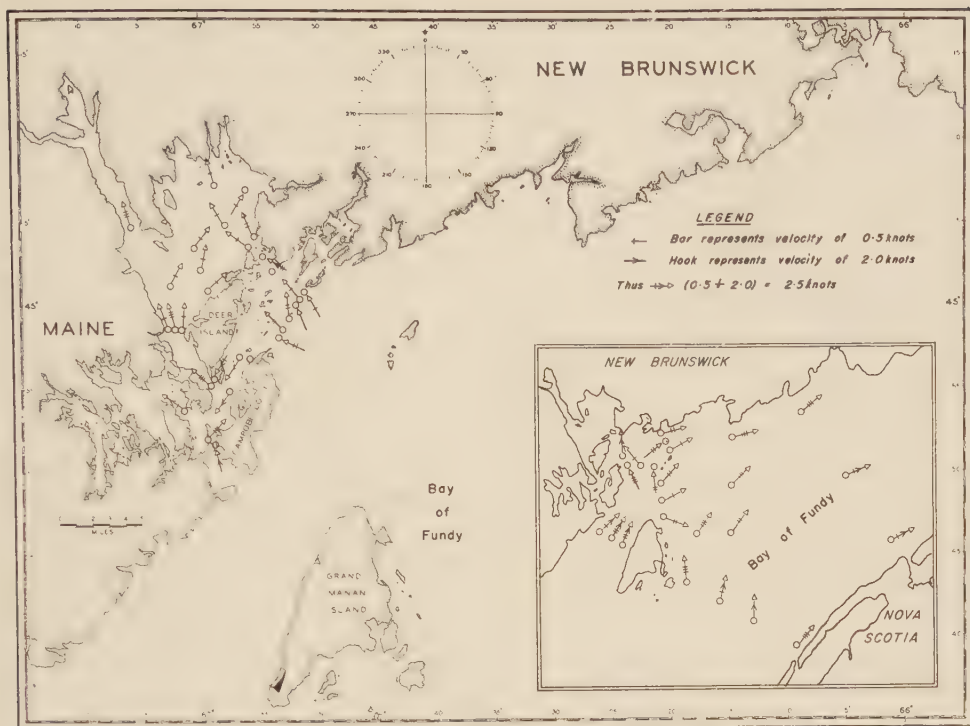


FIG. 10. Tidal streams in Passamaquoddy Bay and Bay of Fundy at half ebb (high water plus 3 hours).

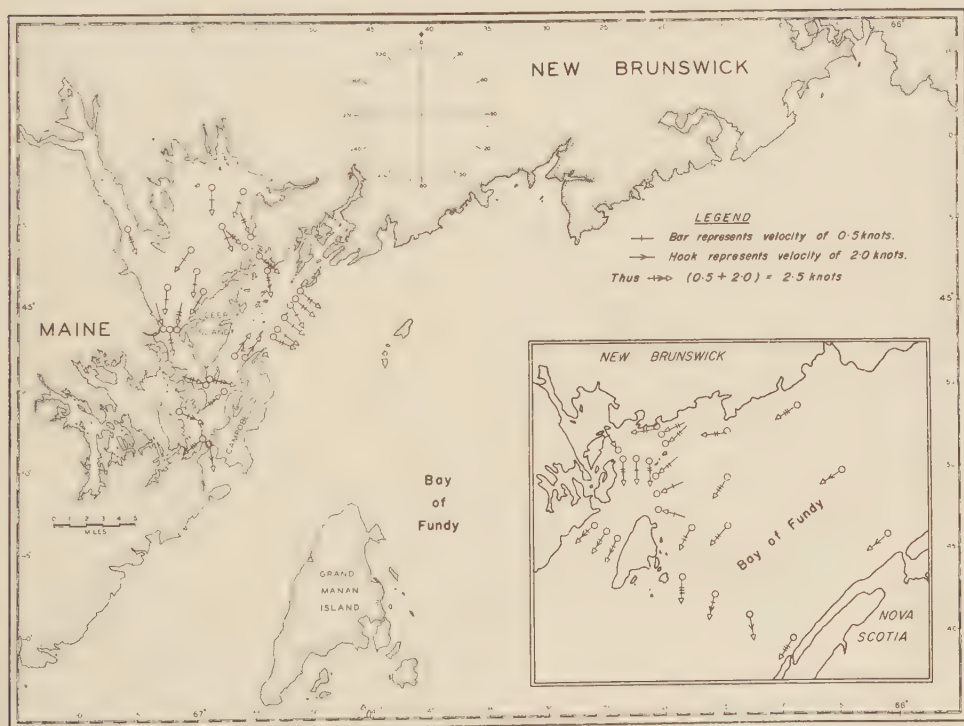


FIG. 11. Tidal streams in Passamaquoddy Bay and Bay of Fundy at half flood (high water minus 3 hours).

for two periods, one at 3 hr before low water, and the other at 3 hr after low water with reference to Saint John Harbour. These were near the time of mean maximum speeds.

Times of slack water occur later in Western Passage than in Letite and vary from 15 to 60 min with some degree of periodicity (Trites and MacGregor, MS, 1959). More than 60% of the intertidal flow into Passamaquoddy Bay is through Western Passage. Peculiarities in the shape of the tidal current curves, as determined by the electromagnetic method (Trites and MacGregor, MS, 1959), suggest the presence of harmonics of the semi-diurnal component and appear to be related to shallow-water effects.

RESIDUAL FLOW

The surface non-tidal circulation in the main portion of the Bay of Fundy is in a counter-clockwise direction (Fig. 12). Inflowing waters from the open ocean hold close to the Nova Scotia coast, while the outflowing waters pass out off the southeast coast of Grand Manan and thence either along the coast of Maine or across the mouth of the Bay of Fundy to the Nova Scotia coast. There is some evidence of seasonal variation in the pattern of flow in the Bay of Fundy (Chevrier and Trites, 1960; Bumpus, 1960). Residual flows are usually less than 2 mi/day in Passamaquoddy Bay, Cobscook Bay, and the approaches. In the Bay of Fundy, flows are variable and at times, in some areas, exceed 10 mi/day (Bumpus *et al.*, 1957; Chevrier and Trites, 1960; Forrester, 1960).

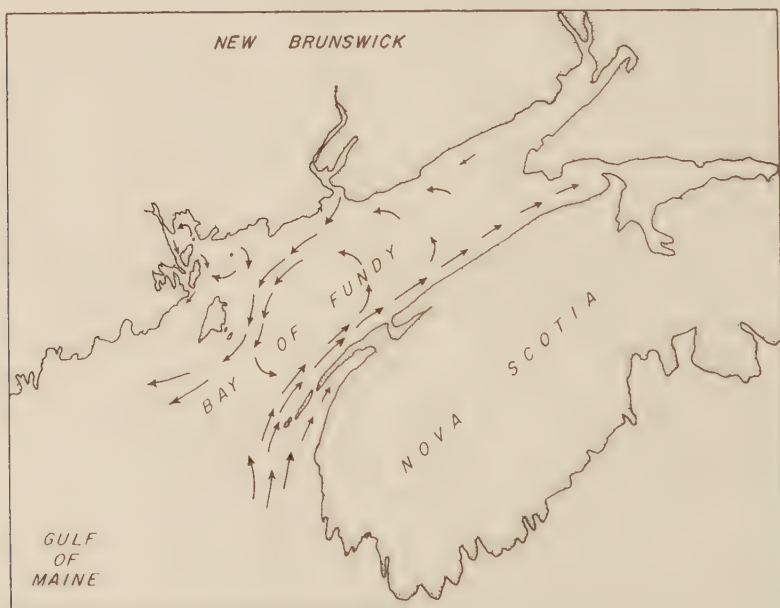


FIG. 12. Non-tidal surface circulation in the Bay of Fundy.

Inside Passamaquoddy Bay, the surface circulation, on the average, appears to be in a counter-clockwise direction around the periphery. Frequently two cyclonic eddies are evidently present, the larger one in the eastern side of the bay, and a smaller one in the Western part of the bay. A relatively free exchange of water occurs between the eddies. There is evidence that the wind modifies this situation markedly. On the whole, wind action is very effective in moving waters of the upper layers and this in turn influences the deeper circulation. In general, it is concluded that winds with a southerly component tend to confine surface waters to Passamaquoddy Bay, while winds from the north and west remove surface waters from the bay. In each instance, there must be a compensating flow at subsurface levels. Since winds vary seasonally in strength and direction from a dominant southwest direction during summer months, to north in winter months, a corresponding effect on circulation in Passamaquoddy Bay can be expected. No clear picture of the net flow through Letite and Western Passages has been established. There is evidence that, on the average, the net flow is outward through Western and inward through Letite. However, there are instances when the net flow appears to be reversed and also times when surface flow is in the same direction in both passages. From theoretic and dynamic considerations, however, it is concluded that the surface water in Western Passage must on the average move outward.

Since Cobscook Bay has very little fresh water discharged into it (average approximately 300 cfs) there is little reason to suspect any marked residual flow. Wind direction and speed, and heating and cooling of the extensive mudflats in the bay, undoubtedly play a role in determining the residual flow. Drift bottles released in the bay usually moved out. It was not uncommon, however, to find that a bottle released outside the bay moved to the inner reaches of Cobscook Bay.

The residual flow through Grand Manan Channel is variable, and it is suggested that winds play an important role in determining the magnitude and direction of flow. Only along the coast of Maine is there evidence indicating that the net flow, at most times, is southwestward.

The circulation in the vicinity of The Wolves has not been determined with certainty. This area, which lies in the offing to the passages, is one where the motion is extremely complex, and difficulty was experienced in measuring the tidal streams with confidence, let alone the residual flow (Forrester, 1960). On the basis of drift-bottle experiments (Chevrier and Trites, 1960), however, there is evidence that an eddy frequently exists, which rotates slowly in a clockwise direction. At other times, this eddy is not evident, and the flow between The Wolves and the mainland reverses direction.

It is concluded that the net flow from the Quoddy Region is, on the average, small. The very marked residual flow resulting from the seaward movement of mixed waters from the Saint John River skirts past Point Lepreau and the Quoddy Region.

TEMPERATURE AND SALINITY

Due to the strong tidal currents vertical mixing of the water proceeds vigorously and hence the seasonal fluctuations in temperature and salinity of the surface layer are relatively small. In the Quoddy Region, the mean annual range of temperature and salinity of the surface layer is approximately 1 to 12°C and 30 to 33‰ (Forgeron, MS, 1959). For inshore areas and in Passamaquoddy Bay the seasonal variations are slightly greater than in the offshore and deep waters. The seasonal pattern of temperature and salinity for two stations, one inside Passamaquoddy Bay and one in the outer Quoddy Region, is shown in Fig. 13.

Mixing in the passages is particularly intense and the water is nearly homogeneous vertically. Grand Manan Channel and the area south and southwest of Grand Manan are areas of very low stratification where the well-mixed waters of the Bay of Fundy are subject to additional local mixing. The greater part of the mixing seems to take place in the shoal area at the southern extremity of the channel and the well-mixed waters are carried northward during the flooding tide. A significant amount of mixing also takes place in the vicinity of Long Eddy Point and West Quoddy Head (McLellan, MS, 1951).

TIDAL PRISM TECHNIQUE

Ketchum (1951) developed a technique for predicting the accumulation of fresh water and mean distribution of salinity in an estuary. To apply the method it is necessary to subdivide the estuary into segments which are horizontally defined by the width of the estuary and the average excursion of a particle of water on the flooding tide. He tested his theory by using data from several areas with vastly different characteristics of tidal range, length of estuary, depth and fresh water discharge. The technique was applied to the St. Croix estuary, Passamaquoddy Bay, and the entire Bay of Fundy (Ketchum and Keen, 1953). The predicted accumulation of fresh water in the St. Croix estuary agreed closely with observation. Flushing times were calculated for the St. Croix estuary and the Magaguadavic estuary from observations taken in June and August 1958. From 43 cruises made in the Quoddy Region in 1957 and 1958, flushing times on a seasonal basis were computed for Passamaquoddy Bay (Forgeron, MS, 1959).

The tidal prism theory assumes complete vertical mixing of the water column, and complete horizontal mixing within each tidal segment. Ketchum (1951) found that in some estuaries the column was incompletely mixed, or that mixing was complete for only a portion of the water column.

Ketchum and Keen (1953) using data taken in August 1951 computed the flushing times of various segments of the St. Croix estuary and found them to vary from a little more than one tidal cycle for the segment near Calais to about three

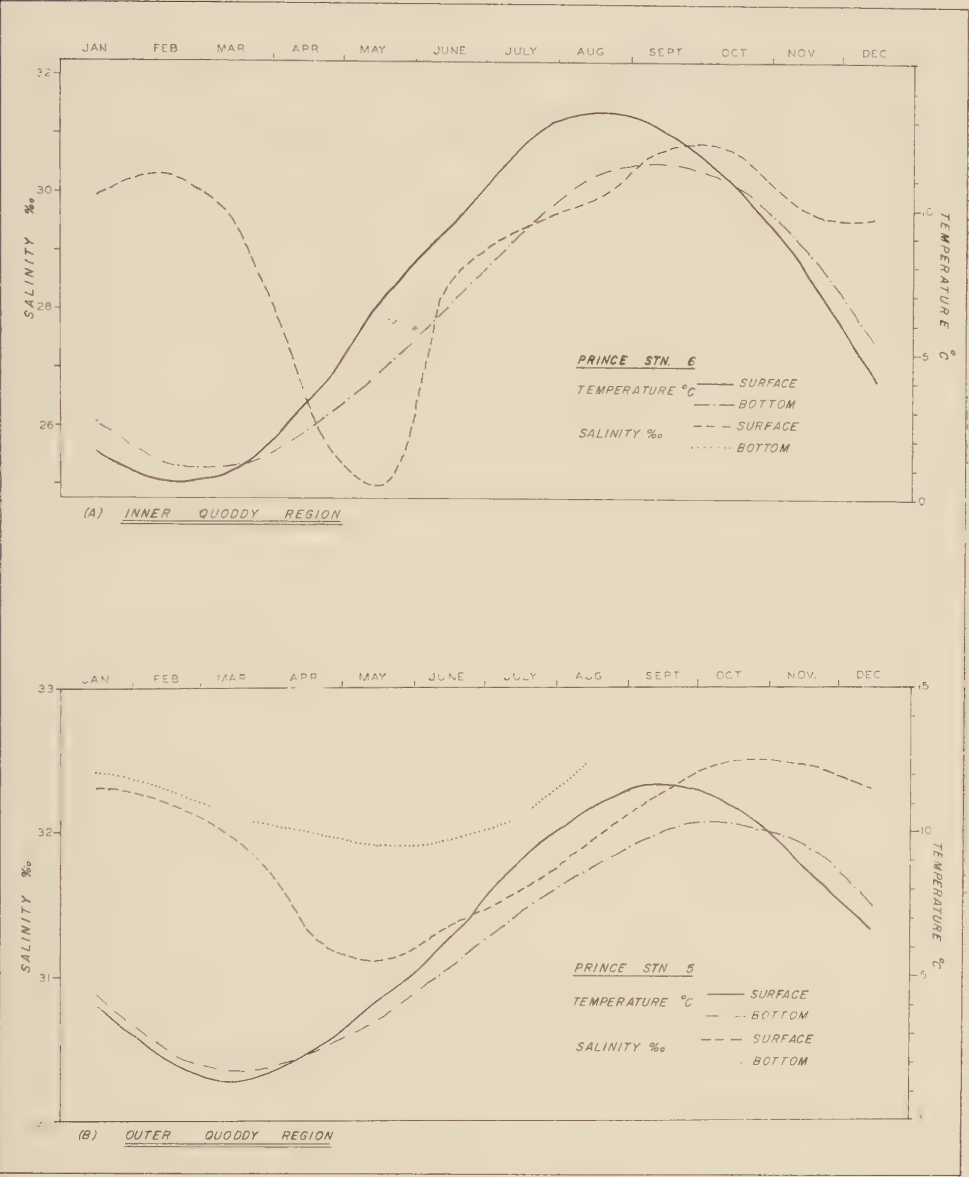


FIG. 13. Seasonal variations in salinity and temperature of surface and bottom waters in inner and outer Quoddy Region.

tidal cycles near St. Andrews. For the entire length of the estuary about 8 days were required to remove one day's river flow. Values computed from observations taken in June and August 1958 (Forgeron, MS, 1959), indicated flushing times of 7 and 6 days respectively.

To aid in the prediction of expected conditions in the St. Croix and Magaguadavic estuaries, if the proposed power project was installed, the tidal prism technique was applied to these estuaries under the new conditions. Sets of salinity distributions were calculated using different mixing hypotheses. From consideration of other areas (Ketchum, 1951; Trites, MS, 1955), it was felt that the most realistic calculation was obtained by considering mixing to penetrate to 10 ft and uniform tidal currents down to 20 ft. The flushing time for the St. Croix estuary, using these conditions and a river discharge of 9.7×10^7 ft³ per tidal cycle, was calculated to be 12 days. By assuming mixing to be complete in the upper 20 ft and velocities zero below 20 ft, the flushing time was computed to be 22 days. In both these cases, it should be noted that a substantial increase in the flushing times from present conditions is predicted. The salinity and percentage of fresh water in the mixed layer for each segment, for the above conditions, are shown in Table I.

TABLE I. Salinities predicted for the mixed layer in the St. Croix estuary, between Calais and St. Andrews, using tidal prism technique, for a river discharge of 9.7×10^7 ft³ per tidal cycle, and a base salinity of 32‰.

Segment:	0	1	2	3	4	5	6
Miles from head (Calais)	2.6	4.7	6.0	8.6	10.4	12.6	13.8
Fresh water, %	100	97	95	38	30	26	20
Salinity, ‰	0	1	2	19	22	24	26

Attention is drawn to the fact that the predicted salinities are mean values. In applying the technique, mixing is assumed to be complete over a given depth. Under natural conditions this is frequently not the case. Surface salinities may be substantially lower than the mean salinity of the seaward-moving surface layer.

The flushing time of the Magaguadavic estuary above Midjik Bluff was computed from temperature and salinity observations taken in June and August 1958 and found to be approximately 2 days. The predicted time, for the new conditions, assuming mixing to be complete to 10 ft and tidal velocities zero below 20 ft, was found to be approximately 5 days.

For the remainder of the high pool Ketchum's prediction technique is not feasible, since it is not a simple estuary with tidal currents oscillating. The location of filling gates in Letite Passage imposes a dominant residual flow in the high pool. The water entering these gates was considered in the same manner as if it were "fresh" water, but it proved unrealistic to carry out segmentation of the high pool, as developed by Ketchum.

OTHER AREAS WITH FEATURES SIMILAR TO PASSAMAQUODDY BAY AFTER DAMS ARE INSTALLED

KENNEBECASIS BAY

Kennebecasis Bay, N.B., is a body of water largely cut off from the sea by a sill near the mouth of the Saint John River. A study of this bay and the Saint John estuarial system was undertaken in 1957 and 1958, since it was conceivable that the physical and biological conditions in this bay are similar to those that might be expected in Passamaquoddy Bay in the event that power dams were installed across its mouth (Trites, 1960).

From this study it was readily apparent that there is a degree of similarity between Kennebecasis Bay and Passamaquoddy Bay when dammed. However, there is one factor that is strikingly different for the two situations. In Passamaquoddy Bay virtually all of the fresh water enters the system from the head of the bay. The fresh water discharged into Kennebecasis Bay at or near its head is comparable to the discharge into Passamaquoddy Bay, but the mouth of the Kennebecasis joins the Saint John River which has an annual discharge approximately 20 times larger than the inflow at the head of Kennebecasis Bay. This influences in large measure the distribution of properties within Kennebecasis Bay. Two sills separate the deep water in Kennebecasis Bay from the Bay of Fundy. The result is that the salinity of the deep layer is nearly 10‰ less than in the Bay of Fundy. Under the conditions of Passamaquoddy Bay with dams installed, there is just one sill, and compared to Kennebecasis Bay which has a large fresh water source at its mouth, there is virtually no fresh water source on the Bay of Fundy side of the filling and emptying gates. It is concluded therefore, that the distribution of properties found in Kennebecasis Bay represents more extreme conditions than will be encountered in Passamaquoddy Bay in the event that power dams are installed. The results of this study are valuable, however, in assisting to bracket the most extreme conditions probable in Passamaquoddy Bay under new conditions.

OAK BAY

Oak Bay, N.B., is an area of the St. Croix estuary (Fig. 14). A few years ago, a portion (approximately 50 acres) of this bay was partially cut off from the sea by a causeway which reduced the tidal exchange. Three conduits, 5 ft in diameter, permit water to flow in during about a 3-hr period near high water. The tidal range is 1 to 2 ft. A small river with a drainage basin of 9 sq mi discharges into the impounded bay. Physically, therefore, there is some similarity between Oak Bay inside the causeway and Passamaquoddy Bay when dammed.

The shellfish investigation of this Board's Biological Station at St. Andrews, N.B., has been studying the area during the past 3 years, and has kindly made data available (J.C. Medcof, personal communication).

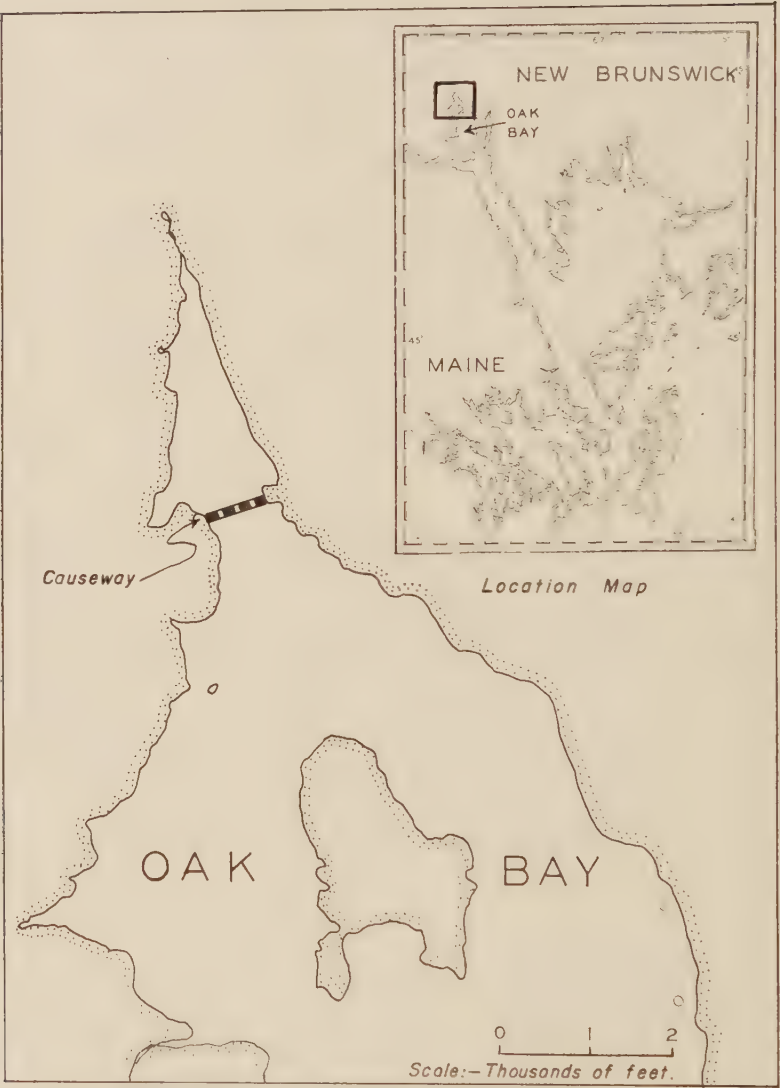


FIG. 14. Oak Bay, showing locations of Causeway.

The salinity and temperature of the bottom water inside the causeway (maximum depth approximately 13 ft) follow closely those outside the causeway, which fluctuate seasonally from about 12 to 30‰ and from 0° to 18°C respectively. Low salinities occur for a brief period during the spring freshet. The surface layer is usually less than 1 ft thick, and varies seasonally in salinity from 1 to 25‰. Maximum recorded depth of surface layer was approximately 3 ft. Temperature of the surface water varies seasonally from less than 0°C in winter to a mean monthly maximum of about 19°C in summer. Ice usually forms in December and except for a small ice-free area near the conduits, remains until March or April. Ice thickness varies from a few inches to greater than a foot during prolonged cold periods. Sufficient observations have not been taken to determine a reliable summer maximum, but the maximum recorded in 1958 was 18.0°C whereas in the previous year it was 20.6°C.

GULF OF ST. LAWRENCE

Tidal amplitudes in the southwestern Gulf of St. Lawrence are similar to those predicted for the new conditions in Passamaquoddy Bay. Mixing due to tidal currents and wind action may on the whole be somewhat more effective in the gulf. Tidal currents in Northumberland Strait reach values of 1 to 1½ knots, and the tidal range is approximately 5 ft. Daily water temperatures, taken at Port Borden, P.E.I., indicate that the mean monthly water temperature ranges from -1.4°C in February to 18.9°C in August (Lauzier, MS, 1953; unpublished data from files, Biological Station, St. Andrews, N.B.). At Ellerslie, Malpeque Bay, P.E.I., minimum temperatures are similar to those at Port Borden, but summer mean maxima reach 21.6°C in July. The mean tidal range is 2½ ft.

In Northumberland Strait, ice usually forms early in December in the shallow harbours. By January the entire strait has fairly heavy ice conditions due in part to ice having moved in from the north. The break-up usually occurs in April (Forward, 1954).

BRITISH COLUMBIA INLETS

An examination of British Columbia inlets is instructive from the point of view of the depth of penetration or thickness of the brackish layer that might be expected in Passamaquoddy Bay. In general, the British Columbia inlets are relatively deep, long, and narrow. The wide ranges of fresh water discharge and tidal currents encountered from inlet to inlet make comparisons with Passamaquoddy Bay worth while. One relatively small inlet (Loughborough) may be taken for illustrative purposes. This inlet has a length of 30 miles and an area of 26 sq mi (Trites, MS, 1955, MS, 1956). The tidal range averages about 12 ft and tidal currents at about midway from the head to the mouth of the inlet are less than 1 ft/sec. The supply of fresh water (yearly average 3430 cfs) during July is approximately 5120 cfs, or 200 cfs/sq mi or 6000 cfs/unit width of inlet. The salinity distribution indicates a surface layer about 7 ft thick and a salinity of

5‰ near the head, about 15‰ at mid-inlet, and 28‰ near the mouth. The thickness of the brackish layer decreases slightly to seaward. In Passamaquoddy Bay the average discharge per square mile is about 40 cfs, which is small compared to that in Loughborough Inlet. Tidal currents appear to be similar in the two areas, but due to the larger fresh water discharge and the dissimilar shapes, one would expect Loughborough Inlet to represent more extreme conditions than might be encountered in Passamaquoddy Bay as a whole under new conditions.

A comparison with only a part of Passamaquoddy Bay, however, indicates a closer similarity to conditions in Loughborough Inlet. The St. Croix estuary, above St. Andrews, has a length of approximately 13 mi and an area of 11 sq mi. The average annual discharge is approximately 2200 cfs, which is equivalent to a discharge of 200 cfs/sq mi and 2600 cfs per unit width. Although the St. Croix estuary is shorter, its discharge per square mile is similar to that of Loughborough Inlet in July.

An examination of several other British Columbia inlets revealed that even for discharges more than five times that of the St. Croix estuary, the depth of penetration of significant proportions of fresh water never exceeded about 33 ft.

DISCUSSION

In the oceanographic study of the Quoddy Region the general features of the tides, circulation, and distribution of properties have been described, but only a qualitative evaluation of the controlling factors has been possible. Without a moderately precise relationship between controlling factors and the circulation, etc., it is impossible to make precise predictions as to what will happen under a new set of controlling factors. Study of the previously mentioned pertinent aspects of other areas, in which some of the factors including tidal amplitude, fresh water discharge, depths and areas bear a degree of similarity to the proposed new conditions imposed on the Quoddy Region, was considered instructive and has facilitated the drawing of conclusions.

Under the proposed project the water level in the high pool will have a "tidal" range averaging 4 ft compared with the present 20 ft. In the low pool the average range will be 8 ft. Outside, the tidal amplitude will be modified only slightly. In the impounded bays, the flow of water will be reduced and consequently vertical mixing will be much reduced. The effect of reduced vertical mixing is twofold, and in each case the tendency will be for increased stratification of the water and a consequent greater seasonal variation in the temperature and salinity of the surface layer.

FLOW CONDITIONS

HIGH POOL. For approximately $9\frac{1}{2}$ of $12\frac{1}{2}$ hr the filling gates will be closed. Water will leave the high pool continuously through the turbines and therefore the motion in Passamaquoddy Bay will be towards Western Passage, where the water is discharged into Cobscook Bay (Fig. 1).

The channel leading to the powerhouse will be approximately 45 ft deep. On the average it would appear that the bulk of the motion in the high pool will occur in the upper 45 ft of the water column. Under these conditions the water level will drop 4 ft in 9 hr compared to the present 19 ft in $6\frac{1}{2}$ hr. Mean velocities should therefore be reduced to approximately one-sixth their present value. However, considering that the bulk of the motion is likely to be confined to the upper 45 ft the mean velocities in this layer will probably be reduced to one-quarter or one-fifth their present values. The present proportion of water entering Western Passage to the total flow into Passamaquoddy Bay is roughly 60%. Under the proposed plan this proportion will be reduced slightly to 55%. During the periods the filling gates are open, velocities in most areas of the high pool should be similar to, but slightly lower, than those of the corresponding present conditions, since the filling rate is only slightly less than the present flooding tide rate (Fig. 4).

At present the residual flow relative to the tidal flow is very small. Under the proposed conditions, the flow in Letite Passage will be unidirectional, and hence on a relative basis at least, the residual flow in Passamaquoddy Bay will be more dominant than at present. A general counter-clockwise circulation in the bay can be expected. The possibility of an eddy in the northeastern part of the bay, and partially distinct from the larger-scale counter-clockwise circulation, cannot be ruled out.

In the estuaries of the St. Croix and Magaguadavic Rivers a net seaward movement of the surface brackish layer and inward movement of the deeper saline water can be expected.

LOW POOL. When the emptying gates are open the water level in the low pool will drop at a rate only slightly less than the corresponding present ebbing tide rate. Therefore, during this period, velocities in Cobscook Bay can be expected to be similar to the present values. The flow in Lubec Narrows will, of course, be reversed from the present conditions, flooding southward and ebbing northward. During the 9 hr that the emptying gates are closed, the water level will rise 8 ft on the average. The water will spread in both directions below the powerhouse, i.e., towards the head and mouth of Cobscook Bay. Mean speeds in Cobscook Bay, west of the powerhouse, will be reduced to approximately one-third the present values. In the outer part of Cobscook Bay, below the powerhouse, the direction of flow will be reversed and speeds reduced on the average to approximately one-fifth their present values. The vertical-longitudinal, non-tidal circulation in Cobscook Bay, west of the powerhouse, is expected to consist of a seaward-moving thin-surface layer and an inward-moving sub-surface layer. Between the powerhouse and the emptying gates (Lubec Channel excepted) the flow will be unidirectional, moving with varying speeds toward the emptying gates.

OUTSIDE. During periods that the emptying and filling gates are closed (6 of $12\frac{1}{2}$ hr) the only significant movement inside the Head Harbour-Bliss Island line will be that required to produce the local tidal prism. The 6 hr is

divided into two periods (Fig. 5): the first one of approximately $3\frac{1}{2}$ hr during the rising tide, starting shortly after half-tide, and the second one on the falling tide, of $2\frac{1}{2}$ hours duration, from just after high water to about half-tide. The flow during these periods, therefore, will be small and inward on the flooding tide and small but outward on the ebbing tide.

During the period the filling gates are open (approximately 3 hr) water will enter Passamaquoddy Bay at speeds only slightly less than at present, and will be in roughly the same proportion as in Letite and Little Letite Passages, and Western Passage (Trites and MacGregor, MS, 1959). Therefore the flow in the offing of Letite Passage will be similar to the present. However, there is no flow directly into the low-pool area from outside. Of the water entering Head Harbour Passage on the flooding tide, at present approximately 60% moves into Western Passage and the remaining 40% fills a volume equal to the intertidal volume of the low pool. Velocities in Head Harbour Passage will be reduced to approximately 50% of their present values, whereas along the Deer Island shore and between Indian Island and Deer Island velocities should be increased moderately due to the reduced cross-sectional area. The area covered inside the high pool by the water that has entered the filling gates per tidal cycle was computed on the bases that it occupied the entire depth, the upper 30 ft, and the upper 15 ft (Fig. 15). The minimal boundary is given by including the entire depth, while the 15-ft layer is considered to represent the maximal boundary. A similar construction was made for the water leaving the emptying gates. It is noted that even the boundary of the 15-ft layer does not extend to the Letite Passage filling gates. Bearing in mind the volume requirements of the Western filling gates, it is considered that under normal conditions only a relatively small proportion of water entering the Letite Passage filling gates will be recirculated water, whereas a relatively large proportion will be recirculated through the Western Passage filling gates. Wind speed and direction, however, may at times alter the normal situation significantly.

While the emptying gates are open, water flow speeds outside near the gates will decrease downstream. Except in the immediate vicinity of the gates, speeds are expected to be substantially reduced from the present values in the area.

In evaluating the probable effects on tidal flow outside the Bliss Island-Head Harbour line it is instructive to consider the present tidal streams and controlling factors for the entire Bay of Fundy. The energy involved in producing the tides in the Bay of Fundy is transmitted into the bay from the Gulf of Maine. It has been deduced by McLellan (1958) that 30.9×10^6 kw of power are transmitted into the Bay of Fundy, and of this, approximately 4% is transmitted into Passamaquoddy Bay. According to McLellan, the bulk of the energy (approximately 90%) is dissipated by friction and escapes from the Bay of Fundy in the form of heat. From the analysis of Ippen and Harleman (MS, 1958) it was concluded that the Bay of Fundy, which could be represented as a damped co-oscillating system, is not highly resonant and that the effect of relatively minor disturbances, such as that of the proposed power project, on the primary tidal wave would be relatively minor.

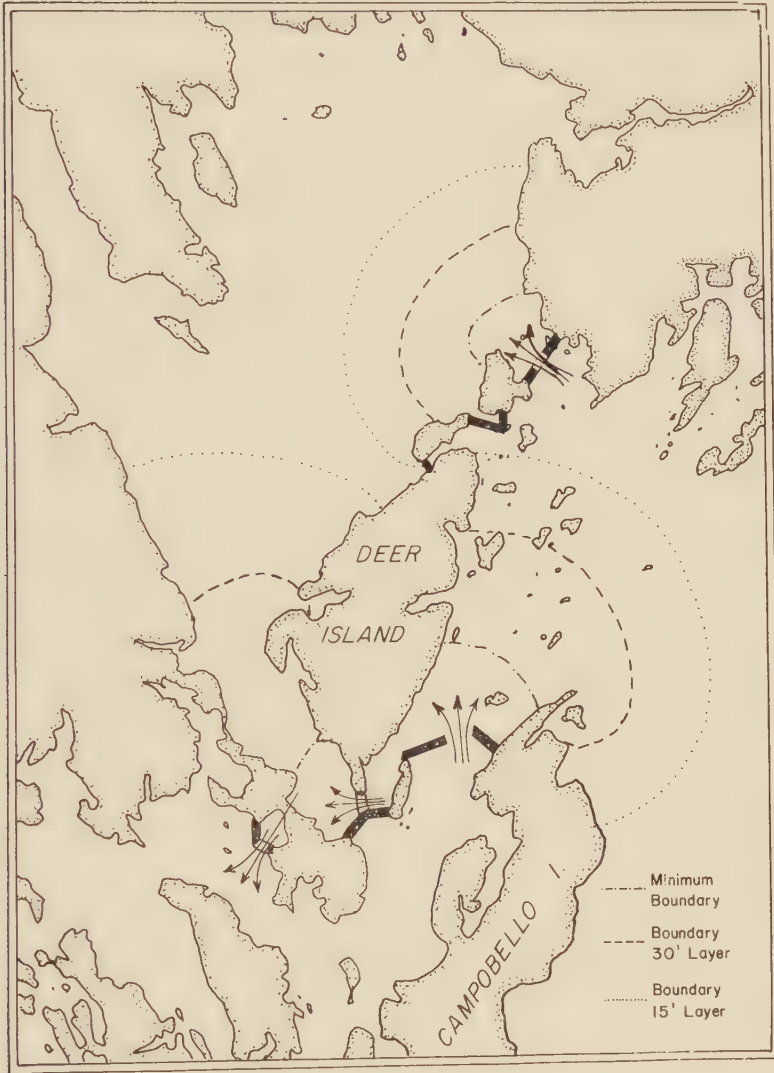


FIG. 15. Area covered by water entering the high pool and leaving the low pool per tidal cycle, assuming it occupied the entire depth, a 30-ft layer, and a 15-ft layer.

The analysis of the Bay of Fundy tidal system reveals no evidence that the partial closing off of Passamaquoddy Bay and Cobscook Bay will interfere significantly with the basic tidal conditions that exists in the Bay of Fundy. Therefore, the same quantity of energy should be transmitted into the Bay of Fundy after the installation of dams as at present. Since the flow into Passamaquoddy Bay and Cobscook Bay will be reduced to approximately 15% of the present value, there will be an excess of energy outside. This will result in an estimated 1% increase in tidal range in the Bay of Fundy. The maximum increase in range should occur at the head of this bay, where McLellan (1958) computed the expected increase to be 0.7 ft. These changes are roughly equal to the changes predicted by Hachey (1934a) on the basis of complete closing of Passamaquoddy Bay.

In the outer Quoddy Region, while the change in tidal range is expected to be insignificant, the change in the tidal streams may be altered measurably. To facilitate a prediction in this regard, use was made of current measurement data (Forrester, 1960) taken in the Quoddy Region. The region was divided into a number of smaller areas whose boundaries were placed so that current measurements could be applied to compute the total flow of water into and out of each sub-area during a flooding tide (Fig. 16). The analysis revealed that for a flooding tide, of the total volume of water ($68 \times 10^{10} \text{ ft}^3$) moving through Grand Manan Channel, a quantity equal to only 31% is required for the intertidal volume in the Quoddy Region (Fig. 16). A volume equal to the remainder, $47 \times 10^{10} \text{ ft}^3$, pushes out through the boundary between Grand Manan and Point Lepreau.

Compared to the water moving through Grand Manan Channel, a quantity less than 10% of the total is required to produce the tidal rise in Passamaquoddy and Cobscook Bays. Under the proposed conditions, this quantity will be decreased to less than 2%. While it is unlikely that the redistribution of energy throughout the cross-section across the Bay of Fundy from the Maine coast through Grand Manan Channel to Nova Scotia will occur uniformly, no reliable way was found to proportion it.

Assuming that the above-mentioned decrease of 8% in volume of water required for the impounded areas was transmitted entirely through Grand Manan Channel, the maximum decrease in the transport through the Channel would be $6 \times 10^{10} \text{ ft}^3$ per flooding tide. To determine the maximum effect likely to be encountered in other areas, it is necessary to choose the upper limit for flow through Grand Manan Channel. It was assumed, therefore, that there would be no change in flow through Grand Manan Channel, and furthermore there would be no change in tidal streams along the Grand Manan shoreline. It is also assumed that the effect of impoundment increases in proportion to distance, reaching a maximum along the Head Harbour-Bliss Island line. The results of these calculations indicate that an increased tidal transport of approximately 10% between Grand Manan and The Wolves, and a decrease of about 20% between The Wolves and Campobello Island, can be expected. The transport into the passages will be decreased to approximately 25% of present

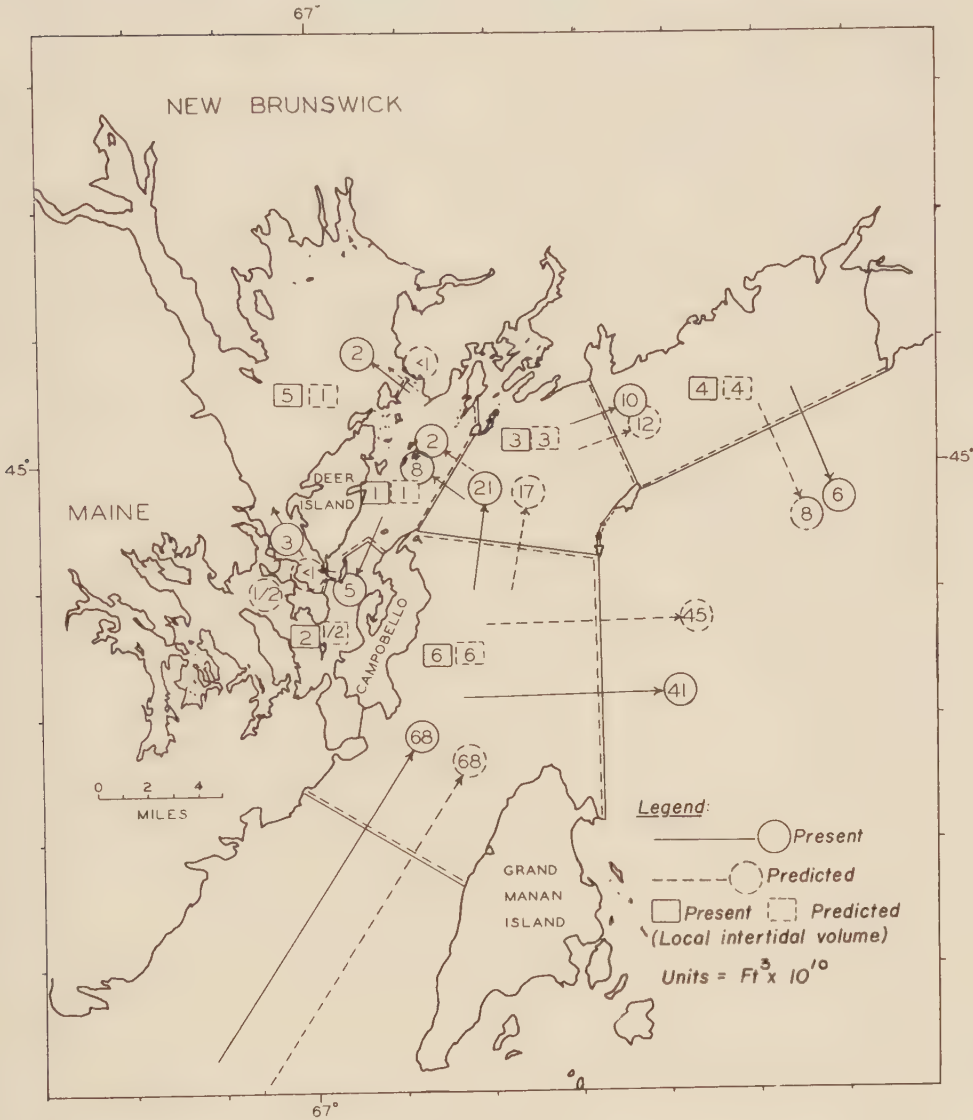


FIG. 16 Volume transports per flooding tide through various sections in the Quoddy Region for present and predicted conditions.

values. Between The Wolves and Beaver Harbour, and The Wolves and Point Lepreau, an increase of 20 and 30% respectively can be expected. Attention is drawn to two points. Firstly, the above computations represent the maximum changes anticipated; secondly, a change of 30% in the flow between The Wolves and Point Lepreau, although relatively large, requires a mean change in speed through the section of only 0.06 ft/sec.

The residual flow in the outer Quoddy Region appears to vary markedly in magnitude, direction and time (Chevrier and Trites, 1960; Forrester, 1960). The wind appears to play an important part in surface movement. There is little evidence to suggest that the amount of mixed water produced in the passages plays any significant role in the circulation away from the passages. Watson (1936) computed the amount of mixing produced by the Quoddy passages and concluded that it amounted to about 6% of the total mixing in the Bay of Fundy. He also concluded that the reduction in this amount of mixing would have very little effect on the general circulation in the Bay of Fundy.

TEMPERATURE AND SALINITY.

GENERAL. Reduced velocities will result in decreased vertical mixing, giving rise to increased vertical stratification and hence to greater seasonal variations in the surface waters.

Certain conclusions as to the mean changes in salinity in the two pools can be derived from a consideration of a simplified model of the new conditions. If it is assumed (a) that the water entering the Letite filling gates is "new" water, (b) that the water entering the Western filling gates is water that has been through the system one or more times, (c) that mixing of the water in each pool is complete both vertically and laterally, and (d) that motion is uniform from top to bottom, then, under steady-state conditions, the principle of conservation of salt enables an expression for the salinity (S_e) of the water leaving the system to be written as:

$$S_e = \frac{V_L}{V_L + R_P + R_C} S_L$$

where V_L = volume of water entering the Letite filling gates,

S_L = salinity of water entering the Letite filling gates,

R_P = fresh water entering the high pool,

R_C = fresh water entering the low pool;

and for the salinity of the high pool (S_p) by:

$$S_p = \frac{V_w S_e + V_L S_L}{V_t}$$

where V_w = volume entering the Western filling gates,

V_t = volume passing through the turbines.

By substitution of the appropriate values for the above quantities, S_e and S_p can be computed under different discharge conditions.

Predicted values of mean salinity have been drawn up (Table II) for conditions of normal river runoff and under maximum seasonal discharge conditions. For comparison purposes, the present values are also shown. In all cases the reduction in salinity under the impounded conditions is small. Maximum lowering, computed on this basis, is in Cobscook Bay and was found to be approximately 3‰, under freshet conditions.

TABLE II. Present and predicted (from salt balance equations) mean salinities (‰), for Passamaquoddy Bay, Cobscook Bay, and outside area, for normal and maximum fresh water discharge conditions.

Fresh water discharge	Passamaquoddy Bay		Cobscook Bay		Outside	
	Present	Predicted	Present	Predicted	Present	Predicted
	‰	‰	‰	‰	‰	‰
Normal	31.43	30.9	31.80	31.0	32.20	32.2
Maximum	30.82	28.7	31.28	28.5	31.72	31.7

HIGH POOL. Moderately marked lateral variation in the surface layer of the high pool is expected. The seasonal variations will be minimal near the Letite filling gates and maximal along the northern shore of Passamaquoddy Bay, in sheltered coves, and in the St. Croix and Magaguadavic estuaries.

From previous considerations, it appears that most of the water entering the Letite filling gates will be "new" water that has not been through the system recently, whereas the Western filling gates will transport a large proportion of recirculated water. Consequently, changes in temperature and salinity inside the Letite filling gates should be altered only slightly from present conditions. Maximum surface salinities should not exceed 30‰. Maximum surface temperatures should not exceed about 14°C. From a consideration of other areas, discussed previously, it appears that the mean monthly maximum temperature averaged over the entire surface layer for the high pool will be in the vicinity of 19°C. The maximum daily temperature for the surface layer in the high pool may reach a somewhat higher value, with about 20°C considered most probable. However, it will vary considerably from year to year, and with location within the high pool. Maximum temperatures can be expected to exceed 20°C in sheltered coves. The coincidence of neap tides, high air temperatures, high insolation, and low wind speeds, at about the time of occurrence of the maximum, could raise temperatures by several degrees in localized areas. The converse of the above combination would reduce the maximum markedly.

The average total fresh water discharge into Passamaquoddy Bay is approximately 4000 cfs of which 50% enters from the St. Croix River. A marked reduction of surface salinity in the St. Croix estuary above St. Andrews can be expected. Quantitative figures as to the extent of this reduction can be concluded only in the broadest terms. In a previous section, a British Columbia inlet was cited as an area somewhat similar to the St. Croix estuary. Although the St. Croix estuary is shorter than Loughborough Inlet, the discharge of fresh water

per unit area and per unit width can be considered comparable, and hence to a first degree of approximation the distribution of properties may be considered similar. In Loughborough Inlet the halocline is found at a depth of about 6 ft, and the mean salinity of the surface layer is 15‰. Salinity increases rapidly with distance towards the mouth. It is expected therefore, that in the area where Oak Bay and the St. Croix estuary join, and also in the vicinity of St. Andrews where the estuary widens abruptly, horizontal salinity gradients in the surface layer will be high. A similar situation can be expected near Midjik Bluff at the mouth of the Magaguadavic estuary.

The St. Croix estuary above St. Andrews, and the northern part of Passamaquoddy Bay are expected to have surface salinities less than 20‰ at most times. The salinity of the remainder of the high pool appears likely to fall within a 20 to 30‰ range. During freshet conditions, surface salinity will probably fall below 20‰ in the high pool, and to less than 10‰ in part of the St. Croix and Magaguadavic estuaries. It is doubtful if the depth of penetration of fresh water will exceed 30 to 50 ft, and it is probable that the bulk of it will be confined to the upper 5 to 15 ft.

Over the past 40 years, extreme ice cover has occurred in two winters. While these two winters represented unusual conditions, it appears that the region is one where, if the surface salinity and vertical mixing decreased substantially, ice formation would probably occur. It is concluded therefore that ice cover in the St. Croix estuary and northern part of Passamaquoddy Bay will occur normally. It is difficult to conclude how extensive this ice cover will be, or what its duration might be, but it appears evident that during particularly cold winters, or ones with heavy snowfall, ice cover will occur over most of the bay.

Salinities and temperatures of the deep layer in Passamaquoddy Bay will probably be altered only slightly with the expected range of temperature falling within 0° and 13°C. Bottom salinities, if altered, would appear to be within 1‰ of present values.

LOW POOL. All saline water reaching Cobscook Bay will be via the turbines and will carry with it the total fresh water discharged into Passamaquoddy Bay. Under present conditions the water in Cobscook Bay, which is in free communication with Western and Head Harbour Passage, is similar in properties to those found in these passages and therefore contains a portion of the fresh water discharged from the rivers draining into Passamaquoddy Bay. However, since this only represents a portion of the fresh water discharge, the mean salinity in the low pool should be lowered under the proposed plan. "Tidal" currents in the low pool will be somewhat higher than the corresponding ones in the high pool. This, combined with thorough mixing of water in passing through the turbines at any instant, will tend to reduce the vertical stratification more than in the high pool. Above Leighton Neck, however, a thin layer not more than some 3 ft thick may be quite brackish and its salinity at times will drop below 20‰.

Minimum bottom salinity which should occur some time after peak fresh water discharge conditions should not drop much below 28‰.

Since stratification is not expected to be as marked in the low pool as in the high pool, the mean range in temperature should be somewhat less. Surface summer maximum in the inner part of Cobscook Bay, however, may reach 20°C while the outer area is unlikely to be much greater than 15°C. Bottom water summer temperatures may increase by 2 or 3 C° due to its source being made up of a mixture of surface water from Passamaquoddy Bay and outside waters. Minimum bottom temperatures appear likely to be lowered only slightly from present conditions. In winter, ice cover can be expected to occur in the inner part of Cobscook Bay.

OUTSIDE. On the basis of previous computations there is little evidence for any pronounced change outside the Head Harbour-Bliss Island line. For the area inside this line, a somewhat greater seasonal variation can be expected, but this is unlikely to exceed a degree or two in temperature and a few parts per thousand in salinity.

DISSOLVED OXYGEN

Under the present conditions, the water in the Quoddy Region is nearly saturated with oxygen at all depths due to the vigorous tidal mixing. Under the proposed conditions, mixing will be decreased inside the impounded bays, and it is probable that the oxygen concentration of the water in the deep basins in Passamaquoddy Bay and Cobscook Bay will be reduced. The rate of replacement of the deep waters, and hence the rate of supply of oxygen to the deep water within the basins, will be a minimum during periods of maximum fresh water discharge into the Quoddy Region. In Kennebecasis Bay, oxygen concentrations in the deep layer at times decreased to less than 40% saturation. It is concluded that, since the Kennebecasis represents a more extreme situation than Passamaquoddy Bay when dammed, oxygen concentration in the high pool is unlikely to fall below 50% saturation. There is no evidence to suggest that low-pool oxygen concentrations should drop below that of the high pool, or that any significant change should occur outside the impounded bays.

SUMMARY AND CONCLUSIONS

The proposed Passamaquoddy power project involves the construction of a series of dams across the mouth of Passamaquoddy and Cobscook Bays. Passamaquoddy Bay, the proposed high pool, will be filled near high water by 90 filling gates and Cobscook Bay, the proposed low pool, will be emptied near low water by 70 emptying gates. Water will flow continuously from the high pool to the low pool through a 30-turbine powerhouse.

The present oceanographic conditions in the region are summarized in broad terms in Table III. Although the general tides, circulation, and distribution

TABLE III. Approximate present oceanographic conditions.

			High pool	Low pool	Outside
Levels (feet)	Mean level (sea)		0	0	0
	Mean range		$\begin{array}{r} +10 \\ -20 \\ -10 \end{array}$	$\begin{array}{r} +9\frac{1}{2} \\ -19 \\ -9\frac{1}{2} \end{array}$	$\begin{array}{r} +9 \\ -18 \\ -9 \end{array}$
	Minimum-maximum elevation (spring range)		-14 to +14	-13 to +13	-13 to +13
Currents	Tidal (ft/sec)		< 1 to 8	< 1 to 8	< 1 to 6
	Non-tidal (mi/day)*		Mostly < 2	Mostly < 2	Variable to 10
Temperature (°C)	Surface	Mean	7	7	7
		Range	0 to 14	0 to 13	1 to 12
	Deep	Mean	7	7	7
		Range	1 to 12	1 to 13	2 to 11
Salinity (‰)	Surface	Mean	31	32	32
		Range	24 to 32	29 to 33	30 to 33
	Deep	Mean	32	32	32
		Range	31 to 33	31 to 33	31 to 33

*1 nautical mi/day = 0.07 ft/sec.

TABLE IV. Probable oceanographic conditions after the dams are installed.

			High pool	Low pool	Outside
Levels (feet)	Mean level		+6	-5	0
	Mean range		4	8	18
	Minimum-maximum elevation		+3 to +11	-11 to 0	-13 to +13
Currents	Gates opened		As present	As present	As present
	Gates closed		Speeds markedly reduced; flow toward Western Passage	Speeds markedly reduced; flow spreads from turbines	Speeds markedly reduced in im- mediate area; slight increase further away
Temperature (°C)	Surface	Mean	Little change	Little change	Little change except in im- mediate area where some- what greater seasonal varia- tion will occur
		Range	< 0 to 19	< 0 to 16	
	Deep	Mean	Little change	Little change	
		Range	0 to 13	0 to 15	
Salinity (‰)	Surface	Mean	< 25	≈ 25	
		Range	< 20 to < 30	< 20 to ≈ 30	
	Deep	Range	29 to 33	28 to 32	

of properties have been described, only a qualitative evaluation of the relationship to the controlling factors has been possible. Without a quantitative relationship between the controlling factors and the circulation, etc., it is impossible to make precise predictions as to what will happen under a new set of controlling factors. In drawing conclusions as to the probable effect of the proposed power project on oceanographic conditions, considerable use has been made of the comparison technique, and hence it should be borne in mind that the predictions given are intended to place only the approximate limits on the changes anticipated. A summary of the gross effects and tendencies that can be expected in water levels, currents, temperatures and salinities in the high pool, low pool, and outside area is given in Table IV.

WATER LEVELS

HIGH POOL. The mean level will be raised about 6 ft with "tidal" range averaging 4 ft. The minimum and maximum range will be $2\frac{1}{2}$ and $4\frac{1}{2}$ ft respectively. The minimum elevation which will occur during neap tides and the maximum elevation which will occur during spring tides will be 3 and 11 ft respectively above mean sea level.

LOW POOL. The mean level will be lowered 5 ft with a tidal range averaging 8 ft. The minimum and maximum range will be $5\frac{1}{2}$ and $9\frac{1}{2}$ ft respectively. The maximum elevation which will occur during mean tides and the minimum elevation which will occur during spring tides will be zero and -11 ft respectively relative to mean sea level.

OUTSIDE. The reduction of flow through the passages will result in a decrease in loading of the Bay of Fundy tidal system and hence give rise to a very slight increase in tidal amplitudes. The maximum range increase which is expected to occur at the head of the Bay of Fundy should be less than 1 ft. Little change is expected elsewhere.

CURRENTS

HIGH POOL. For about $9\frac{1}{2}$ of $12\frac{1}{2}$ hr the filling gates will be closed. Water will leave the high pool continuously through the turbines and therefore the only motion will be towards Western Passage and will be contained mostly in the upper 45 ft. Mean speeds of the upper 45 ft are expected to be about one-fifth of the present values. It is expected that while the filling gates are open, speeds in most areas will be only slightly less than those under the corresponding present conditions. Somewhat higher speeds are likely to occur at mid-depths. A residual counter-clockwise circulation in Passamaquoddy Bay will likely be more marked than at present.

LOW POOL. When the emptying gates are open, velocities will be similar to present values at half ebb. For the remaining 9 hr the velocities should be less than one-third their present value in Cobscook Bay west of the powerhouse and approximately one-fifth between the powerhouse and Friar Roads. The

flow will spread in both directions from the low-pool side of the powerhouse. The vertical-longitudinal circulation in Cobscook Bay west of the powerhouse will be an inward movement of the deeper water and a seaward movement of the surface layer.

OUTSIDE. There is little indication that significant changes in residual flow will extend much beyond the Head Harbour-Bliss Island regions. Tidal streams are expected to be reduced in the approach area of the passages and increased in other areas of the Quoddy Region. The direction of the tidal stream will be altered only slightly while the changes in speed are unlikely to exceed 20% of their present value. For about 6 hr of the tidal cycle, velocities inside Head Harbour-Bliss Island will be very small. During the period the filling gates are open, flow in the Bliss Island region should be similar to the present but flow should be reduced in the Head Harbour region, and increased in the channel between Indian Island and Deer Island. Most of the water entering Western Passage filling gates will be water that has discharged from the low pool. The inflow through the Letite Passage filling gates will be mostly "new" water from outside the dams. The residual flow, which will be more marked than present, will be inward toward Letite and outward from Head Harbour Passage. Wind speed and direction can be expected to play an important role in controlling the amount of water recirculated through the Letite gates.

TEMPERATURE

HIGH POOL. Reduced currents will result in decreased vertical mixing giving rise to increased stratification and hence to greater seasonal variations in the surface waters. These variations will be a minimum near the Letite filling gates (altered only slightly from present conditions) and a maximum along the northern shore of Passamaquoddy Bay and in the St. Croix estuary. Summer maximum at the surface is likely to be in the vicinity of 20°C and winter minimum less than 0°C. Maximum depth of the surface layer would appear to be about 30 to 50 ft and probably only some 5 to 15 ft at most times. Temperatures in the deep layer will likely be altered only slightly with the expected range falling within 0° and 13°C. Ice cover is expected to occur over part of the bay in the winter.

Low pool. Stratification will not be as marked as in Passamaquoddy Bay except in the upper reaches. Surface summer maximum in the inner part of the bay may reach 20°C. In the outer area, it is unlikely to exceed about 15°C. Bottom water summer temperatures may increase by 2 to 3 C°; winter minimum temperatures will likely be lowered only slightly. In winter, ice cover is expected to occur in the inner part of the bay.

OUTSIDE. Little change is expected in the area contiguous to the emptying and filling gates and contained mostly inside the Head Harbour-Bliss Island line where a somewhat greater seasonal variation is anticipated.

SALINITY

HIGH POOL. Mean surface salinity will be lowered. Bottom salinities are expected to be altered only slightly. During freshet conditions surface salinity appears likely to drop below 20‰. At other times of the year surface salinity except in the St. Croix estuary above St. Andrews and the northern part of the bay appears likely to fall within the 20 to 30‰. Maximum surface salinity should occur just inside the Letite filling gates and exceed 30‰. It is doubtful if the depth of penetration of fresh water will exceed 30 to 50 ft; the bulk of it will probably be confined to the upper 5 to 15 ft.

LOW POOL. All saline water reaching Cobscook Bay will be via the turbines and will carry with it the total fresh water discharged into Passamaquoddy Bay. The mean salinity should therefore be lowered. The maximum amount of this lowering (excluding peak runoff periods) should not exceed 3 to 4‰ (i.e., salinity not less than 28‰). It appears unlikely that the bottom salinity will drop below 28‰. Except for the upper reaches of Cobscook Bay, stratification should not be very marked. Above Leighton Neck however, a thin layer, probably not more than a few feet thick, may be quite brackish with salinity at times becoming less than 20‰.

OUTSIDE. The only significant change would appear to be in the area near the emptying and filling gates and inside the Head Harbour-Bliss Island line. Reduction in salinity is unlikely to exceed a few parts per thousand.

DISSOLVED OXYGEN

Under present conditions the water in the Quoddy Region is nearly saturated with oxygen due to the vigorous tidal mixing. Under the proposed conditions mixing will be decreased inside the impounded bays and it is probable that the oxygen concentration of the water in the deep basins in Passamaquoddy Bay and Cobscook Bay will be reduced. The rate of replacement and hence the rate of supply of oxygen to the deep water within the basins will be at a minimum during periods of maximum fresh water discharge into the Quoddy Region. However, by comparison to Kennebecasis Bay which is considered to represent more extreme conditions than will be found in the high pool, it is concluded that the dissolved oxygen concentration is unlikely to fall below 50% saturation.

ACKNOWLEDGMENTS

The author is indebted to his fellow workers for their assistance and constructive criticisms. He also wishes to thank the International Passamaquoddy Engineering Board for providing the engineering material dealing with the power project.

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Competition for Food Between Redside Shiners (*Richardsonius balteatus*) and Rainbow Trout (*Salmo gairdneri*) in Two British Columbia Lakes^{1,2}

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ABSTRACT

The distribution, movements, behaviour and food of trout and shiners in Paul and Pinantan Lakes were studied to determine the items and mechanisms of interspecific competition between them. Data from recent years were compared with data for years when trout alone inhabited the lakes.

No interspecific aggression was observed. The possibility that the two species were competing for space was discounted. Stomach contents of shiners in Pinantan Lake revealed a marked qualitative diurnal food cycle. In Paul Lake, shiners have drastically reduced the *Gammarus* population relative to its pre-shiner abundance, forcing trout, as well as the shiners themselves, to shift their diets to other foods. This overgrazing was caused by the concentration of large numbers of shiners over the shoals where *Gammarus* are also present in their highest concentrations, and the ability of shiners to pursue food deeper into the weeds and to graze an area more thoroughly than trout. In Pinantan Lake, shiners have apparently reduced the density of *Daphnia* to a point where trout are unable to feed on them as rapidly as in pre-shiner years. The ability of both species to utilize many types of food tends to reduce the intensity of competition.

The study demonstrates how false implications may arise from an appraisal of competition not initiated until after the effects of competition have been observed. If observations had not been made on Paul Lake until after competition had been observed, the importance of *Gammarus* as an item of competition would probably have been overlooked and the whole competitive relationship misconstrued.

Environmental factors and behaviour were shown to be important influences on the dynamics of competition. The physical and biological environment and the distribution and behaviour of competitors may be in states of continual flux in which case the niches of the competitors cannot be considered constant.

INTRODUCTION

FIELD STUDIES of interspecific competition are usually carried out in situations where two or more species have been in association for some time prior to the study period. In consequence there is often no opportunity to observe the sequence

¹Received for publication August 22, 1960.

²Based in part on a thesis submitted in partial fulfilment of the degree of Master of Science in the Department of Zoology and the Institute of Fisheries, University of British Columbia.

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of events which transpired in the early stages of the interaction between the two species. The long-term studies on Paul Lake, British Columbia (Mottley, 1932; Rawson, 1934; Larkin *et al.*, 1950; Larkin and Smith, 1954; Crossman and Larkin, 1959; Crossman, 1959a,b) provide a good background for the present observations on the competitive relationship between the reidside shiner (*Richardsonius balteatus*) and the rainbow trout (*Salmo gairdneri*).

The trout of Paul Lake and of Pinantan Lake (which is next above Paul Lake in the chain) were the only species of fish in the system before 1930. Some-time thereafter, reidside shiners were introduced into Pinantan, and in the period 1945 to 1950 they were carried downstream into Paul Lake. There are at least three aspects to the interaction between the two species of fish: predation of shiners on trout fry, competition between shiners and juvenile trout for environmental resources, and predation by large trout on shiners. The present study was directed to an assessment of where, when, how, and for what environmental resources shiners compete with young trout.

A marked decrease from 1946 to 1957 in the growth rate and survival of Paul Lake trout less than 20 cm fork length leaves little doubt that the presence of shiners had adverse effects on young trout (Larkin and Smith, 1954; Crossman and Larkin, 1959). The same is apparently true in Pinantan Lake, although no observations were made there in "pre-shiner" years. Among trout below 20 cm fork length an unusually slow growth rate, similar to that observed in Paul Lake after shiners had become established, was found in Pinantan Lake in 1952 (MacLeod, MS, 1957) and during the present investigation in 1958—the only two years of observation. It seems reasonable to infer that shiners had adverse effects upon trout in Pinantan Lake similar to those observed in Paul Lake.

The field work on which this study is based was carried on at Paul and Pinantan Lakes during the summer of 1958. All of the field records and collected material are at the Institute of Fisheries at the University of British Columbia.

CHARACTERISTICS OF THE LAKES

The two lakes have some important limnological differences although they share a common climate and are adjacent in the drainage system. Some of the limnological characteristics are listed in Table I. Both lakes have one major inlet and a single surface outlet. Rawson (1934) discussed the limnology of

TABLE I. Limnological characteristics of Paul and Pinantan lakes.

	Paul	Pinantan
Area	960 acres; 237 ha	161 acres; 40 ha
Shoreline development	5.50	3.89
Maximum depth	182 ft; 56 m	62 ft; 19 m
Mean depth	112 ft; 34 m	31 ft; 9.5 m
Dissolved electrolytes	216 ppm	238 ppm
Altitude	2500 ft; 760 m	2860 ft; 870 m

both lakes, concluding that Paul was typically oligotrophic but with relatively high productivity because of extensive shoal areas, and that Pinantan was a highly productive eutrophic lake.

The shoal areas of both lakes are well developed with extensive growths of *Chara*, *Myriophyllum*, *Potamogeton* and filamentous algae. These shoal areas harbor large populations of fish food organisms and contribute a major portion of the total bottom fauna of both lakes (Rawson, 1934; Larkin *et al.*, 1950). Although organisms are most abundant in shallower areas, there is a substantial bottom fauna to the greatest depths in Paul Lake. From 1934 to 1949 the amphipods *Gammarus* and *Hyalella* declined in abundance, in association with an increase in the trout population. From 1949 to 1958 there was a further five-fold decline in abundance of amphipods associated with the introduction of redbreasted shiners. Rawson observed no bottom organisms below the thermocline in Pinantan Lake and attributed this absence to severe oxygen depletion. In 1959 visible organisms were completely absent from samples taken from Pinantan Lake at depths of only 8 and 10 feet (2.5 and 3.0 m) in both June and August. However, the abundance of organisms was high in the shoal areas, increasing in volume and variety to the shallowest inch.

The mat of *Chara* and algae was so dense near shore that sampling with an Ekman dredge was impractical. Samples comprising 2 litres of *Chara* were collected with a rake; 11 from June 10 to 13 and a further 11 from August 20 to 25. They indicated a predominance of Odonata and Gastropoda, with a large number of *Planaria* in the June samples (Table II). The total volume of

TABLE II. Mean percentage volume of bottom organisms in 2-litre samples of *Chara* from depths under 10 feet (3 m) in Pinantan Lake, June and August, 1958.

1958	Odonata larvae	Trichoptera larvae	Hirudinea	Gastropoda		<i>Hyalella</i>	<i>Planaria</i>
				<i>Physa</i>	<i>Planorbis</i>		
June	32.3	1.7	1.1	11.7	7.1	3.4	27.0
August	77.4	+	+	17.4	+	4.3	+

organisms in the June samples was 3 times as large as in August. As in Paul Lake in recent years, the amphipods were relatively scarce, *Gammarus* being entirely absent from the samples although present in the lake.

The predominant zooplankters in both Paul and Pinantan lakes are *Daphnia* and *Diaptomus*. In Pinantan Lake blooms of *Aphanizomenon* and *Anabaena* are common, and *Chaoborus* occurs in the plankton at night. Neither extensive blue-green algae blooms nor *Chaoborus* occur in Paul Lake.

Summarizing: although Paul and Pinantan lakes differ somewhat limnologically, the food resources for rainbow trout and redbreasted shiners in both lakes are concentrated in the shoal areas and the plankton.

FOOD OF SHINERS

Crossman (1959a) has described the nocturnal offshore movements of shiners. Accordingly, sampling for shiners was conducted both near shore and off shore over 24-hour periods in Pinantan Lake. Two gillnets of $\frac{1}{2}$ -inch (13-mm) stretched mesh were set for 1-hour periods at intervals of 4 hours, one at the edge of the shoal area and the other approximately 100 yards (90 m) offshore. The stomach contents of 168 shiners caught in the nets between July 6 and September 6 were examined. Of these, 150 were taken in the period August 20 to 26. In preliminary observations, groups of shiners were held without food for various lengths of time before their stomachs were examined. Whereas 90% of the stomach contents from fish killed immediately on capture were identifiable, only 15.5% were identifiable after the fish were held foodless for an hour, and 3.7% after 2 hours. It was concluded that almost all food had been eaten within 2 hours before capture. Hence any diurnal change in food habits would easily be detected in the stomach contents of the fish sampled from 1-hour sets made at 4-hour intervals.

A marked diurnal change in foods was discovered. Figure 1 shows a shift in dominance from *Daphnia* to algae during the day and back to *Daphnia* at

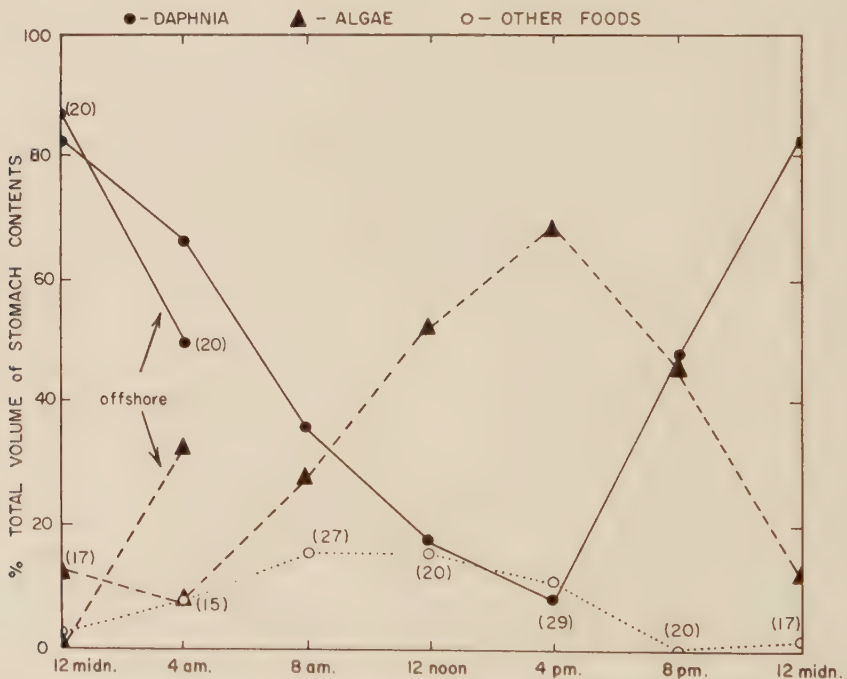


FIG. 1. Percentage total volume of *Daphnia*, algae and other foods in the stomach contents of shiners taken at 4-hour intervals over 24 hours. Unidentified food is not included among the "other foods". Numbers in brackets give sample sizes.

night in the diet of Pinantan Lake shiners. There was no significant diurnal variation in the quantity of food eaten. The stomachs of 37 shiners taken at midnight contained 92.5% *Daphnia* and 6.2% algae (mainly *Spirulina*, *Spirogyra* and *Nodularia*). In contrast the stomachs of 29 shiners taken at 4 p.m. contained only 19.1% *Daphnia* and 69% algae.

The shift is more striking for offshore fish than for those on the shoals. At midnight, 20 offshore fish had virtually no algae in their stomachs while 17 shoal fish had 14% algae, but by 4 a.m., 20 offshore fish had 34% algae in their stomachs while 15 shoal fish had only 8% algae. All shiners move back to the shoal at dawn; shiners were caught offshore only in the midnight and 4 a.m. sets.

Zooplankton, consisting almost entirely of *Daphnia pulex*, made up 58.1% of the diet and algae contributed 26.4%. Other food included *Hyalella*, various aquatic and terrestrial insects, *Planorbis* and *Physa*. None of these other foods ever contributed more than 12% of the diet of a group of fish caught at one time, and together they made up only 6.1% of the total diet. About 10% of the food was too well digested to be identified.

Stomachs of shiners collected in 1959 in Paul Lake by the writers and in various previous years in both lakes by members of the British Columbia Game Commission were also examined. The deterioration of all but the 1959 stomachs made accurate stomach analysis difficult. Apparently there was no marked qualitative diurnal variation in the feeding habits of Paul Lake shiners similar to that found in Pinantan shiners. Collections of 10 shiners taken at 2 p.m. and 2 a.m. on August 1, 1959, both contained approximately 15% *Gammarus* and 85% terrestrial insects. Terrestrial insects were also the main food of 20 shiners taken in Paul Lake on July 25, 1950.

No algae or *Daphnia* were found in the stomachs of any Paul Lake shiners taken between 1950 and 1959. This is in sharp contrast to Pinantan Lake where *Daphnia* and algae contributed over 85% of the total diet in 1958.

FOOD OF TROUT

The diet of trout in Paul Lake has been reported extensively by Rawson (1934), Larkin *et al.* (1950), Larkin and Smith (1954) and Crossman and Larkin (1959). Prior to the entrance of shiners into the lake, trout of all sizes shared a mixed diet of near-shore bottom organisms, plankton and terrestrial insects. From 1934 to the 1946-1949 period there was an increased utilization of plankton and a noticeable decline in the occurrence of amphipods, both trends being construed as evidence of heavier grazing of food resources by a larger trout population. After 1949, shiners became an increasingly important food item, largely replacing plankton in the diet of trout over 10 inches (25 cm) fork length. Smaller trout had diets similar to those of the pre-shiner period except for a notable decline in the proportion of stomachs containing amphipods (Fig. 2).



FIG. 2. Proportion of rainbow trout stomachs containing amphipods, Paul Lake, 1931 to 1957. (Extended from Larkin *et al.*, 1950.)

The stomach contents of 335 trout taken from Pinantan Lake in the summer of 1958 suggested a similar diet to that of Paul Lake trout in recent years (Table III). For fish under 10 inches, *Daphnia* made up over 60% of the diet throughout the July to September period. Bottom organisms (chiefly dragonfly nymphs and chironomids) were important in the remainder of the diet except for later in the season when terrestrial insects contributed substantially. Shiners contributed 70% of the diet of trout over 14 inches fork length, the remainder being bottom organisms and *Daphnia* which were more important as food sources late in the season. *Gammarus* and *Hyallela* were recorded in the stomach contents but were a negligible food item. The trout of intermediate size (10 to 14 inches) showed lower utilization of shinners and a greater dependence on *Daphnia*, a diet intermediate between those of smaller and larger sized trout.

Diaptomus was absent from the stomachs of both trout and shinners in both lakes despite the fact that it is a very abundant plankton in both lakes. The very low availability to salmonids of *Cyclops*, a similar copepod, has been mentioned by Southern (1933), Lindstrom (1955) and Nilsson (1955).

AREAS AND TIMES OF SPECIES OVERLAP

Crossman (1959a) described the seasonal and diurnal movements of shinners in Paul Lake. Their movements in Pinantan Lake were similar although the trends were not as clear-cut as those observed in Paul Lake.

Data on the distribution of shinners in Pinantan were derived from direct observations made day by day during June through August 1958, as well as from gillnet sets made just off the shoal and offshore.

The shinners first appear on the shoals in schools in May or June. Observations commenced on Pinantan Lake in the middle of June. The shinners on the shoal exhibited the same vertical and horizontal stratification noted by Crossman

TABLE III. Average volume of stomach contents of Pinantan Lake rainbow trout according to month and length-group in 1958. The number in brackets under each length group is the number of trout in that group for the whole year. The number in brackets beside the month is the number of trout of all sizes in that month.

a: number of stomachs containing each food item;

b: percentage of stomachs containing each item;

c: volume of each item as a percentage of the total volume of food.

Fork length	July (104)								August (162)								September (69)							
	Shiners	<i>Daphnia</i>	Anisoptera nymphs	Chironomid larvae	Other insect larvae	Other bottom organisms	Terrestrial insects	Miscellaneous	Shiners	<i>Daphnia</i>	Anisoptera nymphs	Chironomid larvae	Other insect larvae	Other bottom organisms	Terrestrial insects	Miscellaneous	Shiners	<i>Daphnia</i>	Anisoptera nymphs	Chironomid larvae	Other insect larvae	Other bottom organisms	Terrestrial insects	Miscellaneous
6-10 in 15-25 cm (122)	a	2	21	4	2	4	2	9	7	48	8	24	8	1	5	10	-	21	4	4	2	-	11	12
	b	6	69	11	6	11	6	25	13	86	14	43	14	2	9	18	-	70	13	13	7	-	37	40
	c	8	61	9	+	7	+	14	22	63	9	1	+	+	4	2	-	65	2	2	1	-	18	13
10-14 in 25-36 cm (116)	a	12	8	6	4	3	2	3	14	33	16	12	12	3	2	13	2	17	3	3	2	-	4	2
	b	40	27	20	13	10	7	10	23	54	26	20	20	5	3	21	8	68	12	12	8	-	16	8
	c	53	14	13	1	10	4	4	33	28	18	+	14	5	+	2	6	31	30	1	3	-	21	8
14+ in 36+ cm (97)	a	25	3	11	1	4	-	9	29	19	16	16	7	1	5	14	4	5	5	5	-	-	4	4
	b	65	8	29	3	10	10	24	64	42	36	36	16	4	11	31	29	36	50	36	-	-	29	29
	c	76	1	9	+	3	-	4	68	10	15	1	1	+	2	3	30	20	40	+	-	-	6	5

(1959a) in Paul Lake and Lindsey (1953) in Rosebud Lake: the smallest shiners were closest to the shore and the larger fish were progressively deeper and farther offshore. On cloudy days all but the newly hatched fry, $\frac{1}{2}$ inch long, moved into deeper water just off the shoal. The shiners were most frequently seen in schools of from 30 to 500. Occasional individuals swimming lethargically by themselves were observed throughout the summer. Dead shiners were also seen frequently. Presumably some disease was affecting these fish, although it was not identified. Incidence of the tapeworm *Ligula*, which varies from almost 100% to almost zero in various years, was negligible in 1958.

In early July the vertical stratification for all but the fry broke down gradually. The largest fish left the shoals first. An estimated 50% of the fry remained on the shoal during this general offshore movement.

By the end of August the schools had reformed and stratified on the shoals again. The lake was treated with toxaphene in early September. Presumably the fish would have moved offshore en masse in October as they had been observed to do in previous years by the lodge owner and by Crossman (1959a) in Paul Lake. Nothing is known of their winter distribution. Local residents report that they collect around holes cut in the ice during the winter.

Previously described around-the-clock gillnetting showed that, similarly to Crossman's findings in Paul Lake, the shiners in Pinantan Lake spread out over the surface waters of the lake as nightfall approached, and moved back to shore at the first light of morning. During the night they were caught from the surface down to a depth of 25 feet (7.6 m).

At 11:30 p.m., June 25, about 1/20 of the daytime numbers were seen by flashlight on the shoal, randomly distributed according to size horizontally and vertically, except for fry which were still in schools within 6 inches (15 cm) of the surface.

There is a considerable background of information on movements and distribution of trout in Paul Lake. Tagging studies done in 1952 and reported by Crossman (1959b) indicated that "at least in 1952, there were no discrete populations of trout at any one place at any one time" (except during the spawning migration) in Paul Lake. "The trout seemed to move about freely from place to place over the length of the lake, at times moving from one end to the other."

Observations and results of gillnetting on both Paul and Pinantan Lakes indicate that during the summer the large trout, 10 inches (25 cm) and larger, tend to stay around and below the thermocline. Mottley and Mottley (1932) stated that the older fish in Paul Lake "seek great depths" during the summer. By contrast, recently planted hatchery fingerlings (2-5 inches, 5-13 cm) were seen in large numbers on the shoals in as little as a foot (30 cm) of water in July 1959, often swimming in company with schools of shiners.

The only area where trout and shiners were both observed in numbers during the summer was on, or just off, the shoals in the upper 20 feet (6 m) of water. Trout, but not shiners, also ranged below this depth. No trout were ever taken along with shiners in the offshore gillnet sets. Competition for food thus seems

to be centred mainly around the shoals between shiners and young trout. However, co-occupancy of an area is not a prerequisite for competition if the items competed for are mobile. Considerations discussed in a later section suggest that the offshore night grazing by shiners in Pinantan Lake may be another component of competition, acting to reduce the numbers of zooplankters which might move towards the shoals or into deeper water where they would become available to trout.

Shiners occupy the shoal areas from July to September, making excursions offshore at night, on cloudy days and for a short period in July. The remainder of the year they are apparently predominantly offshore where they, like the trout, are believed to be relatively inactive, and little competition for food probably occurs.

COMPETITION FOR FOOD

a. PAUL LAKE

The abundance of the amphipods, *Gammarus* and *Hyallela*, is a conspicuous feature of most of the small lakes of the Kamloops district in British Columbia. The decline in their abundance, first in response to increased grazing by trout, and then further after the introduction of redbreasted shiners, has been a noticeable feature of the Paul Lake studies. Figure 2 indicates the decline in occurrence of these amphipods in trout stomachs from 1931 to 1957. Mottley and Mottley (1932) reported that in 1931 trout stomachs contained an average of 167 amphipods, and Rawson (1934) indicated that they contributed 39.8% of the total volume of the food eaten. In the 1946 to 1949 period, amphipods contributed only 9.4% of the food of trout (Larkin *et al.*, 1950), and from 1955 to 1957 even individual gammarids were rarely present in the stomachs of trout (Crossman and Larkin, 1959).

Pen feeding experiments, with *Gammarus* collected from nearby Louis Lake, were carried out to observe the feeding behaviour of trout and shiners on this apparently highly vulnerable food organism. In each pen 500 *Gammarus* were released and given adequate opportunity to seek shelter in a quantity of *Chara* which had been washed previously to remove all visible organisms. In a 24-hour period 10 trout from 3 to 6 inches (7.6–15 cm) long, reduced the initial number of *Gammarus* to 119; 10 shiners from 1½ to 3 inches (3.8–7.6 cm) long reduced the initial number to 105, while 315 *Gammarus* were recovered from a control pen containing no fish. There is thus little doubt that each species found *Gammarus* acceptable as food. The *Gammarus* left by the shiners averaged 3 times as large as those left by trout.

The possibility of physical interaction between trout and shiners during their co-exploitation of *Gammarus* was examined. Field observations suggest that interspecific aggression does not occur between the two species. Crossman (MS, 1957) observed no aggressive activity and commented that the shiners "appeared to be more efficient feeders and when a trout and shiner darted after the same food item, the shiner invariably got it and while shiners would move

right into the shore to feed, trout appeared to come only into water no shallower than 15 inches".

In the course of the 1958 and 1959 summer observations many trout 3 to 5 inches (76–127 mm) long were seen swimming in company with, or in and out of, schools of shiners in 2 to 8 feet (0.6–2.5 m) of water. There appeared to be no interspecific behavioural activity; each species apparently being oblivious to the other. Shiners, however, moved noticeably faster and hence ranged over a wider area per unit time in search of food than trout.

Shiners 1–3 inches long (25–76 mm) and trout of 3–6 inches (76–152 mm) were held in enclosures for observation and feeding experiments. Four-sided pens, 6 × 6 × 5 feet deep (2 × 2 × 1.6 m), built of door screen on a wooden frame, were placed on *Chara* beds near shore and anchored firmly to the bottom in about 4 feet (1.2 m) of water. The bottoms of the pens were open, hence the enclosed fish were swimming over natural *Chara* beds and had access to the bottom. There was no observed difference in the behaviour of the two species when together and when alone. Trout remained singly at the sides or corners of the pen just above or down among the dense weed growth, except when they were feeding. Shiners stayed in compact groups in a volume of about 8 cubic feet (0.24 m³) just above and among the tips of the weeds. Only when frightened by quick movements of the observer did they scatter down into the weeds. The school moved very slowly over the whole area of the pen, often staying more or less in one spot for 10 minutes or more, but never seeming to favour any spot nearer the sides or corners any more than the centre of the pen. Figure 3 illustrates the characteristic disposition of the two species of fish when they were not feeding in the enclosures.

Figure 4 illustrates the characteristic arrangement of the individuals of the two species when given food. Approximately 2000 *Gammarus*, most of which were alive, were placed in pens already containing trout and shiners. These observations were repeated four times during July and August 1958 with virtually identical results.

The shiners, being at first higher above the weeds, were on the whole faster to notice the *Gammarus* and faster to start feeding than the trout. When the trout started feeding they ranged higher above the weeds than the shiners and the shiners ranged deeper into the weeds than the trout. Trout seemed to take *Gammarus* "at random", making erratic rushes here and there, often ignoring amphipods close by and rushing after others farther away. Shiners appeared to feed more efficiently and methodically than trout. They moved as a school eating every *Gammarus* near them that was visible to the observer as well as making feeding movements at objects too small for the observer to see. (This was not so with the trout. The observer could invariably see the objects on which they were feeding). The shiners fed more slowly than the trout, making approximately half the number of feeding movements per individual per unit time as did the trout. They often spat out and rejected larger *Gammarus*.

Trout often chased and nipped each other during the feeding period but were never observed to chase or nip shiners. Occasionally a trout and shiner would

collide while moving in search of food. As the trout were larger and moving faster, the shiners were usually pushed aside in this collision. However, incidents of this nature appeared accidental and were infrequent. On one occasion only one 2-inch shiner chased a 4-inch trout for about one foot horizontally.

On some occasions small trout spat out large *Gammarus* three or four times before finally swallowing them or rejecting them completely. On some such occasions a shiner would eat the amphipod before the trout had a chance to mouth it again. This was the only type of overt competition for the same food item which was observed.

It has been stated that trout would not forage down among the weeds in search of food as the shiners did. A second line of evidence in Paul Lake supports this observation. *Gammarus* were abundant down to a depth of 50 metres in pre-shiner years of low trout abundance (Rawson, 1934). When the trout population was increased as a result of heavy stocking, *Gammarus* below the *Chara* zone decreased markedly in abundance while in the *Chara* zone they decreased only slightly (Larkin *et al.*, 1950). *Chara* appears to provide amphipods with relatively effective shelter from the predation of trout.

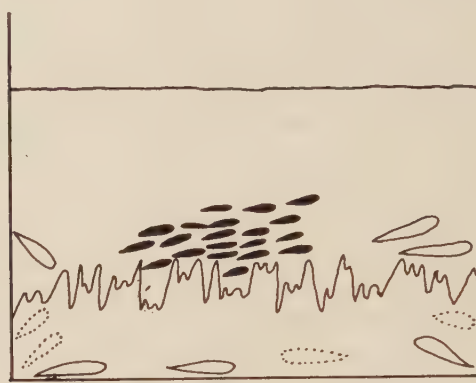
Attempts to estimate the size of the population of shiners in Paul Lake have not met with much success. All who have attempted population estimation have agreed that the shiner population was extremely large in both Paul and Pinantan. Lindsey (1953) found the numbers of shiners in Paul Lake too great for accurate estimation with practical fin clipping experiments, but stated that in 1950 the number was somewhere between 5 million and 100 million. Larkin and Smith (1954) estimated the number in 1952 as "several million". At the same time the trout population was recruited from hatchery plantings of 200,000 fry per year, augmented by natural spawning (Larkin *et al.*, 1950). The population of trout over 6 inches (15 cm) fork length was in the range of 15,000 to 20,000. Even estimating the population of small trout generously as 200,000, the shiners were perhaps 50 times as abundant as young trout. The numerical preponderance of shiners was apparent from direct observation on the shoal areas in the midsummer. Schools of several thousand were common.

The grazing potential of this population of shiners, their readiness to eat amphipods, and their concentration over the shoal areas strongly suggest that they were capable of substantial inroads on food resources previously exploited only by trout.

b. PINANTAN LAKE

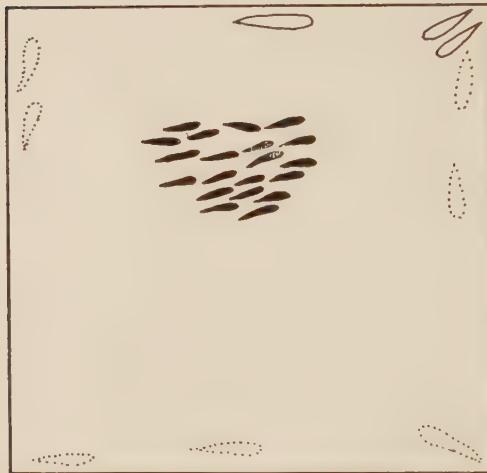
In Pinantan Lake the shiner population was also obviously very much larger than the population of small trout. There were relatively few amphipods compared with Paul Lake when shiners were introduced, according to Rawson (1934). He attributed this to the absence of an extensive *Chara* zone in Pinantan⁵.

⁵Since this time a very rich and extensive *Chara* zone has developed in Pinantan Lake. As this plant affords amphipods considerable protection from the predation of trout it is probable that a large amphipod population would have developed along with the *Chara* had shiners not been present to graze them down.



A. SCHEMATIC SIDE VIEW

- SHINER
- TROUT
- ⋯ TROUT HIDDEN IN WEEDS



B. VIEW LOOKING DOWN ON PEN

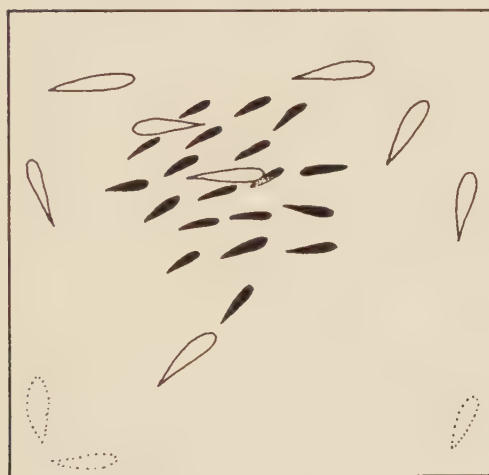
FIG. 3. Diagram of the distribution of trout and shiners in the observation pens when not feeding.

Trout remain at the sides or corners of the pen just above or down among the weeds. Shiners hover in a compact school above and among the weed tips, favouring neither centre nor sides of the pen.



A. SCHEMATIC SIDE VIEW

- SHINER
- TROUT
- TROUT HIDDEN IN WEEDS



B. VIEW LOOKING DOWN ON PEN

FIG. 4. Diagram of the distribution of trout and shiners in the observation pens when feeding. Trout range higher in the water than shiners. Shiners go deeper into the weeds for food than trout. (Trout pictured in the weeds have just returned from feeding excursion and do not feed while in the weeds.) Shiners still school though less compactly than when not feeding. Trout do not school. The two species intermingle as though oblivious to each other.

There were still very few amphipods in the lake during the study period and *Daphnia* was the main item of food of both shiners and young trout.

It is impossible to determine the effects of the shiners on the abundance of *Daphnia* in Pinantan Lake directly, as there are no data from pre-shiner years. However, their probable effects may be inferred from a comparison of the present situation with one described by Ricker (1937) where competition among sockeye salmon fingerlings for *Daphnia* resulted in significantly reduced growth rates in years of large salmon populations.

Direct observations of the densities of shiners on the shoals in both Paul and Pinantan Lakes suggest that their concentrations in the two lakes were approximately the same. The concentrations of shiners present at night in the pelagic feeding ground in Paul Lake vary between 1 and 18 per 6 cubic metres (calculated using data from Lindsey, 1953). This approximates the concentration of sockeye in Cultus Lake in August 1932 noted by Ricker (2 in 7 m³).

In August, 1958, adult shiners in Pinantan Lake consumed about 2200 *Daphnia* per day⁶—4.5 times as many per individual as the sockeye in Cultus Lake as estimated by Ricker. The concentration of *Daphnia* in Pinantan Lake was about 1.2 per litre—less than half the concentration observed in Cultus Lake, although the turnover rate of plankton may be higher in eutrophic Pinantan Lake than in oligotrophic Cultus Lake.

Intraspecific competition for *Daphnia* occurred at the described levels of food, feeders and feeding in Cultus Lake. Since the food requirements of young rainbow trout and sockeye fingerlings are similar, the above comparison suggests competition for *Daphnia* between shiners and young trout in Pinantan Lake. This may account for the observation that the growth rate of young Pinantan trout was even slower than the shiner-retarded growth rate of young Paul Lake trout.

SUMMARY OF RESULTS

Interspecific aggressive behaviour was not a factor in competition for food between trout and shiners at Paul and Pinantan Lakes. No chasing or nipping was observed either in the lakes or in the observation pens.

Shiners in Pinantan Lake had a marked qualitative diurnal food cycle.

Five observations suggest that trout are at a disadvantage when competing with shiners for amphipods in Paul Lake:

1. Shiner's range deeper among the weeds in search of food than trout, cropping off many bottom organisms before they reach areas above the weeds where they are available to trout.
2. Shiners eat food items smaller than the smallest items taken by trout, grazing off many amphipods before they reach a size at which they are

⁶This estimate is based on the previously described digestion rate experiments, volumetric stomach analysis, and a count of the number of *Daphnia* per cubic centimetre of pure *Daphnia* in a trout stomach. Stomach contents of trout, rather than shiners, were used for the last figure because the pharyngeal teeth of shiners fragment their food so much that the enumeration of individual plankters is impossible.

available to trout. Shiners graze heavily on immature amphipods, presumably leaving fewer to survive long enough to reproduce and replenish the population.

3. In the summer during the day, shiners are concentrated directly over the shoals. Trout tend also to be near the shoals, but farther offshore and in deeper water, not so close to the main source of amphipods.
4. Shiners feed more methodically than trout, searching areas more thoroughly for their food.
5. There are probably 50 or more shiners for each trout in the lake.

The competition for *Daphnia* in Pinantan Lake is not as readily studied and described as the competition for amphipods in Paul Lake. Several facts are apparent however. Shiners feed on *Daphnia* in the upper pelagic region during the night. Trout do not occupy this area. It is suggested, however, that the grazing of shiners is sufficiently intense that the amount of zooplankton moving into deeper water or into shoal areas, where it becomes available to young trout, is reduced significantly.

DISCUSSION

Competition in nature is usually first recognized only after its results have become apparent. Usually a noticeable change in one of the competing populations (e.g. reduction, extinction, emigration) must occur before the observer becomes aware that competition is taking place. At this time one cannot pick out the features of the competitors' biology that differ from those existing before competition began. Discovering the items and mechanisms of competition under these circumstances is like trying to discover the plot of a novel from the last chapter.

The present situation in Paul Lake serves to illustrate how false conclusions may be drawn from a delayed appraisal of competition. In recent years amphipods have been scarce in the lake, and have formed only a small fraction of the stomach contents of trout and shiners. On the basis of this observation alone an observer would hardly suspect that amphipods had been the most important item of competition. What is more, as there is relatively little overlap in the present feeding habits of the two species, one might conclude that competition for food was negligible. The present situation is an example of Hartley's (1948) statement that "the finding of different foods in different species is not irrefutable proof of the absence of competition, unless it can be shown that all selection of foods is by choice alone from diverse superabundant food stocks all equally accessible to the species studied". Observations made before and during the first phase of competition showed that shiners and trout were not feeding by choice alone. They had been forced by the depletion of amphipods to replace them by other, presumably less preferred foods.

This shift in the diets of trout and shiners in Paul Lake since competition began serves to caution against assuming that the present feeding habits of the two species in Pinantan Lake tell the whole story of competition there. Possibly the most important original items and mechanisms of competition in Pinantan were quite different from what they were at the time of this study.

It is possible that if the other foods in Paul Lake were reduced by shiners to a level of abundance comparable to that in Pinantan Lake, the shiners would shift to *Daphnia* as their main food. A second phase of competition, paralleling that described in Pinantan Lake, might then ensue. Nilsson (1955) reports that char in Swedish lakes turn from a diet of bottom organisms to plankton when the former become scarce.

However the complex of environmental variables, which influences the intensity and the items of competition discourages prediction of future developments in either lake. An epizootic of unknown etiology resulted in a mass mortality of shiners in Paul Lake in August 1958. Subsequently, in 1959, shiners were found far less frequently in trout stomachs. Amphipods were significantly more abundant in the trout diet in 1959, presumably because there were fewer shiners to graze them down.

Infestation by the tapeworm, *Ligula*, in shiners varies from almost 100% to almost nil in the lakes from year to year. *Ligula* infested shiners are not only sluggish and more vulnerable to the predation of trout, but they also have extremely small amounts of food in their stomachs compared with uninfested fish. Individual shiners probably consumed significantly less food in years when they were heavily parasitized.

Yearly differences in rainfall and atmospheric temperature cause almost a two-fold difference in the summer heat income of Paul Lake (Larkin *et al.*, 1950). Fluctuations of this magnitude might be expected to result in significant year-to-year differences in food production, fish distribution and spawning success of trout and perhaps shiners—all of which are factors in the intensity of competition. Nilsson (1955) has ascribed year-to-year differences in the foods of trout and char in three Swedish lakes to the effect of differences in temperature and lake levels in different years, at least in part. In the space of any one year seasonal changes in temperature and oxygen profiles, light and precipitation, and diurnal changes in light, combine to complicate further the dynamics of competition. Year-to-year, seasonal, or diurnal changes occur in: rate of food production; relative abundance of various types of food; accessibility of food (e.g. *Gammarus* are probably less vulnerable to predation by trout and shiners in years and seasons of highest *Chara* growth); reproductive rates of competitors; density of competitors in relation to the density of food; distribution of competitors with respect to each other and with respect to food; size distribution of competitors (relevant because of the propensities of different size groups for different foods). Both competitors and items of competition are thus non-randomly distributed in both space and time in a highly complicated fashion.

Larkin (1956) has commented on the vague demarcation of ecological zones in freshwater environments and the lack of sharp demarcation of fish faunas

within these zones. "Freshwater communities would seem to be characterized by more breadth than height in the pyramid of a food chain; a complexity in horizontal organization." A better illustration of this statement⁷ than the present one could hardly be imagined. Both shiners and trout eat almost all the organisms available in the lakes—including each other. At different times of the day, and of the year, fish may be found leading a pelagic, shoal, or bottom existence, with their food habits varying accordingly. The feeding habits of trout and shiners in various lakes described in the literature reveal an enormous range of dietary tolerance. The ability of both species to change their distributions and diets tends to reduce intensity of competition. While amphipods have been severely depleted in Paul Lake, both trout and shiners have found substitutes for them in their diets. That this new diet is not as satisfactory as the old one for young trout may be inferred from their slower growth rate—but large trout now grow faster than before as a result of feeding on shiners. Hence the difference in abilities of large and small trout to change their diets results in opposite effects of competition within different size groups of the same species.

To summarize, interspecific competition among fishes may be continually shifting in intensity and emphasis. The physical and biological environment and the distribution and behaviour of the competitors may be in states of continual flux, in which case the niches of the competitors cannot be considered constant.

ACKNOWLEDGMENTS

Financial support for this study came from the National Research Council in Canada.

The construction of apparatus and collection of field material was greatly assisted by Messrs E. Stenton and J. A. Boone. I am indebted to Messrs T. Miura and W. E. Ricker for aiding with the data analysis.

Appreciation is extended to those members of the Kamloops detachment of the British Columbia Fish and Game Branch who gave their help, particularly Mr P. Mulligan.

Dr C. C. Lindsey's valuable suggestions are gratefully acknowledged.

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⁷Recently G. S. Myers (1960, *Evolution*, **14**(13): 394-396) has pointed out that this assertion is based on certain temperate faunas and is not universally applicable, especially to tropical continental rivers.

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Herring Movements in the Bay of Fundy and Gulf of Maine, 1957 and 1958^{1,2}

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ABSTRACT

During 1957 and 1958, 137,469 herring were tagged in the southern part of the Bay of Fundy and the western part of the Gulf of Maine. These fish were immature and ranged in mean total length from 9.9 to 20.0 cm and in age from 1 to 3 years. Recovery of 3,582 (2.6%) tagged individuals showed that herring moved in and out of Passamaquoddy Bay irregularly throughout the summer and autumn with some tendency to concentrate at the head of this bay. Outward movement reached a peak in July when there was a considerable movement eastward towards Point Lepreau. Herring moved into Passamaquoddy from as far south as Grand Manan and from as far east as Point Lepreau. Little interchange of herring took place between the Passamaquoddy area and the coasts of Maine and Nova Scotia. The greatest straight-line distance from release to recovery points was 55 miles. More than half of the recaptures were made within 2 miles of the tagging sites and nearly two-thirds within 5 miles. About 28% of the recaptures were made within 1 week after tagging and 63% within 2 weeks. The average time before recapture was 12 days in 1957 and 17 days in 1958. The longest time between release and recapture for both years was 165 days. Drift bottles released with tagged herring showed no apparent relationship between herring movements and surface drift. The results of tagging support a general conclusion that the proposed Passamaquoddy tidal power structures will have no significant effect on the herring fisheries of the Passamaquoddy area.

INTRODUCTION

IN THE PASSAMAQUODDY AREA of southwestern New Brunswick and eastern Maine, there is a large fishery for young, immature herring "sardines". In 1958 landings in Charlotte County, New Brunswick, and Washington County, Maine, were approximately 68,000,000 lb or nearly 25% of the total herring landings in the Bay of Fundy and Gulf of Maine for that year. Catches are used chiefly for the production of canned sardines. Fish meal and oil, pet food and bait are other products.

To provide details of young herring movements, tagging experiments were carried out in 1957 for the first time along the Atlantic coast of North America as part of the International Passamaquoddy Fisheries Board research program (Hart and McKernan, 1960). These experiments were continued in 1958. Major responsibility for the project was assumed by the Fisheries Research Board of Canada and 49 of 59 tagging experiments in the two years were conducted from the St. Andrews Biological Station. The Boothbay Harbor laboratory of the United States Bureau of Commercial Fisheries carried out 10 taggings and assisted in 20 others.

Reports on the 1957 experiments were published by McKenzie and Tibbo (1958) and McKenzie and Skud (1958). The present paper gives the results of the 1958 experiments and discusses herring movements in both years in relation to distance, time and direction.

¹Received for publication, September 28, 1960.

²International Passamaquoddy Fisheries Board, 1956-59. Scientific Report No. 30.

MATERIALS AND METHODS

An opercular tag (Fig. 1) developed for smelt by McKenzie (1950) was used for all herring taggings in both 1957 and 1958. Tags were made of various shapes to identify different taggings. Experiments were conducted to determine the colour that would yield the best returns. On June 17, 1958, 220 scarlet and 250 maroon tags were attached to dead fish entering Connors Bros. sardine plant at Black's Harbour, N.B. Returns of 165 (75%) scarlet and 128 (51%) maroon tags showed that scarlet was a better colour to use. A further experiment was carried out using live fish from a weir at Navy Island near St. Andrews, N.B., on July 25, 1958, when 968 "sardines" were tagged with scarlet tags, 986 with maroon tags and 964 with yellow tags. Returns of 13 (1.3%) scarlet, 0 (0.0%) maroon, and 6 (0.6%) yellow, again showed scarlet to be the best colour to use. The 1958 tagging operations (Table 1) give returns of 1,278 (4.5%) scarlet, 1,506 (2.2%) maroon and 6 (0.2%) yellow tags.



FIG. 1. Tagging method and equipment. Type of tag and point of attachment shown in inset.

TABLE I. Recaptures from herring taggings, March 3 to October 17, 1958. (S = Scarlet tag, M = Maroon tag, Y = Yellow tag).

Location	Date	Fish tagged Number	Recaptures		Total recaptures	
			Complete data	Incomplete data	Number	Per- centage
Long Island Bay, N.B.	Mar. 3	1951(M)	7	0	7	0.4
Red Head Harbour, N.B.	Mar. 11	1965(S)	54	1	55	2.8
East Wolf Island, N.B.	Mar. 18	2966 (S M)	143	0	143	4.9
Seely Cove, N.B.	Mar. 20	1913(S)	10	0	10	0.5
Maces Bay, N.B.	Apr. 9	1913(M)	4	0	4	0.2
Crow Cove, N.B.	Apr. 10	971(M)	1	0	1	0.1
Fox Island, N.B.	May 2	2863(S)	43	1	44	1.5
Loring Cove, Me.	May 9	2970(M)	234	0	234	7.9
Birch Cove, N.B.	May 16	2974(S)	708	6	714	24.0
Little Kennebec, Hope Is., Me.	May 16	2992(M)	41	2	43	1.4
Mascarene Shore, N.B.	May 22	2479(S)	91	5	96	3.9
St. Andrews Point, N.B.	May 29	2956(S)	144	5	149	5.0
New River Island, N.B.	June 4	1937(S)	14	0	14	0.7
Bean Island, N.B.	June 10	1889(S)	67	3	70	3.7
Mill Cove, N.B.	June 17	1399(M)	180	6	186	13.3
Moose River Cove, Me.	June 17	2959(M)	30	2	32	1.1
Bean Island, N.B.	June 19	2960(M)	112	18	130	4.4
Griffin Cove, N.S.	June 24	2405(M)	3	0	3	0.1
Sandy Cove, N.S.	June 25	1126(M)	0	0	0	0.0
Spider Cove, N.B.	July 2	2984(M)	335	27	362	12.1
St. Andrews Point, N.B.	July 3	2945(M)	31	1	32	1.1
Bocabec Bay, N.B.	July 4	2993(M)	112	23	135	4.5
Chandler Bay, Me.	July 8	1480(M)	0	1	1	0.1
Sprucehead Island, Me.	July 9	1970(M)	1	0	1	0.1
East Bay, Me.	July 10	2976(M)	63	0	63	2.1
Great Chebeague Island, Me.	July 11	2104(M)	1	0	1	0.04
Linekin Bay, Me.	July 17	2933(M)	1	0	1	0.03
St. Andrews Point, N.B.	July 25	2918(S M Y)	19	0	19	0.7
Dipper Harbour, N.B.	July 31	2959(S)	19	0	19	0.6
New River Beach, N.B.	Aug. 1	2970(M)	59	0	59	2.0
Eagle Island, N.B.	Aug. 6	1472(M)	2	0	2	0.1
Cedar and Laireys Is., Me.	Aug. 19	2128(M)	0	0	0	0.0
Seely Cove, N.B.	Aug. 20	2531(M)	11	0	11	0.4
Sprucehead Island, Me.	Aug. 20	2949(M)	1	0	1	0.03
Gleason Cove, Me.	Aug. 26	2623(M)	44	0	44	1.6
McCann Cove, N.B.	Aug. 29	2951(S)	24	0	24	0.8
Holt Point, N.B.	Sept. 4	1494(M)	23	0	23	1.5
Passamaquoddy Bay, N.B.	Sept. 5	2982(M)	50	1	51	1.7
Long Pond Bay, N.B.	Sept. 23	1460(Y)	0	0	0	0.0
Two Island Harbour, N.B.	Sept. 24	1460(S)	3	0	3	0.2
Lobster Cove, Me.	Oct. 15	2169(M)	2	0	2	0.09
Capitol Island, Me.	Oct. 17	2935(M)	1	0	1	0.03
Sub-totals:						
Scarlet tags		28,308	1,257	21	1,278	4.5
Maroon tags		69,242	1,425	81	1,506	2.2
Yellow tags		2,424	6	0	6	0.2
Totals		99,974	2,688	102	2,790	2.8

The herring tagged in 1958 were obtained from weirs and seines as in 1957. During most of the taggings, samples from the same catches were taken for length and age analyses. Samples taken within the Passamaquoddy area in 1958 varied in mean total length (calculated on the basis of 10 mm groupings) from 9.9 to 19.8 cm and in age from 1 to 3 years. The overall mean length for all 1958 samples was 14.1 cm (15.6 cm in 1957). Table II shows the size range and mean length of each sample obtained. There was no indication that size variation influenced the tagging results. Figures 3 to 11 illustrate the results of representa-

TABLE II. Size distribution of herring tagged in 1958.

Date	Locality	Size range	Mean length
		<i>cm</i>	<i>cm</i>
Mar. 3	Long Island Bay, N.B.	8-17	12.4
Mar. 11	Red Head Harbour, N.B.	7-16	11.4
Mar. 18	East Wolf Island, N.B.	9-17	13.3
Mar. 20	Seely Cove, N.B.	8-19	12.3
Apr. 9	Maces Bay, N.B.	8-16	11.6
Apr. 10	Crow Cove, N.B.	7-16	9.9
May 2	Fox Island, N.B.	9-21	12.5
May 9	Loring Cove, Me.	9-18	13.1
May 16	Birch Cove, N.B.	10-20	15.1
May 16	Little Kennebec, Me.	9-14	10.9
May 22	Mascarene Shore, N.B.	9-19	12.7
June 4	New River Island, N.B.	8-16	9.9
June 10	Bean Island, N.B.	10-21	14.0
June 19	Bean Island, N.B.	11-20	14.0
July 2	Spider Cove, N.B.	12-20	15.7
July 3	St. Andrews Point, N.B.	11-26	16.2
July 4	Bocabec Bay, N.B.	11-20	15.0
July 8	Chandler Bay, Me.	12-20	14.1
July 9	Sprucehead Island, Me.	14-20	16.8
July 10	East Bay, Me.	14-24	16.8
July 11	Great Chebeague Is., Me.	9-25	17.9
July 17	Linekin Bay, Me.	13-19	15.9
July 25	St. Andrews Point, N.B.	12-20	15.2
Aug. 1	New River Beach, N.B.	11-28	15.8
Aug. 19	Cedar & Laireys Is., Me.	9-22	18.0
Aug. 20	Seely Cove, N.B.	15-28	19.8
Aug. 20	Sprucehead Is., Me.	14-23	17.5
Sept. 4	Holt Point, N.B.	15-25	18.7
Sept. 5	Passamaquoddy Bay, N.B.	15-24	18.3
Oct. 15	Lobster Cove, Me.	9-18	12.1
Oct. 17	Capitol Island, Me.	9-17	13.4

tive taggings in 1957 and 1958. Only recaptures with complete information are shown in the figures or considered in the text. Distances from tagging sites to recovery positions were measured in straight lines.

TAGGING AND RECAPTURES, 1958

Table I shows that from March to October 1958, 99,974 "sardine" herring were tagged in 39 locations (Fig. 2) on 42 occasions. Sixteen locations were

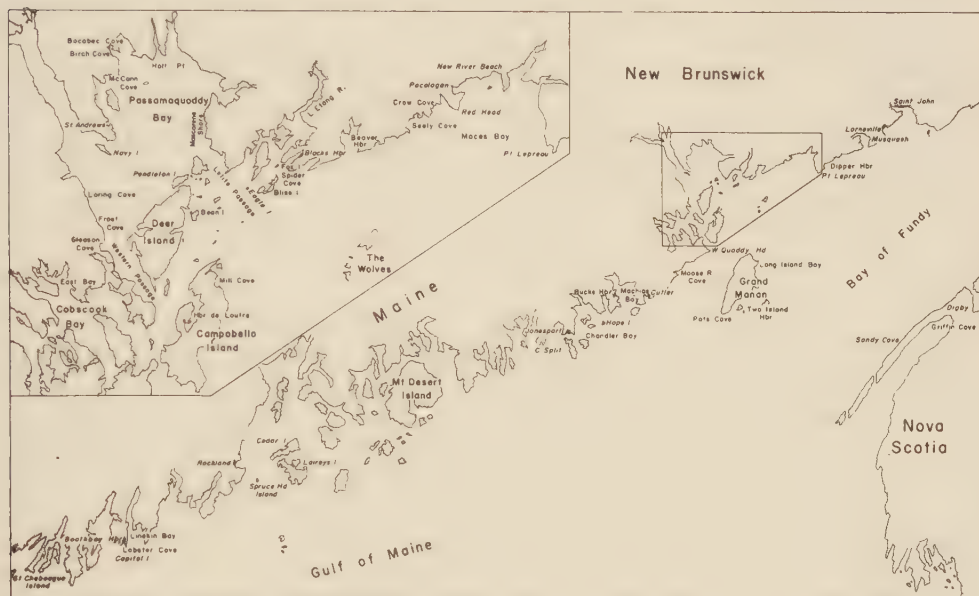


FIG. 2. Map showing location of tagging sites and other places mentioned in the report.

in or at the mouth of Passamaquoddy Bay, 10 were located westward along the coast of Maine as far as Great Chebeague Island, 8 were eastward along the New Brunswick shore as far as Dipper Harbour, 3 were off Grand Manan and 2 off Digby Neck, Nova Scotia. A total of 2,790 (2.8%) tags were recovered, 2,688 with complete data concerning time and place of recapture.

LONG ISLAND BAY TAGGING

On March 3, 1,951 purse-seined herring were tagged at Lat. $44^{\circ}44'27''$ N, Long. $66^{\circ}43'05''$ W. Of the 7 recaptures, 4 were made in the tagging locality within 2 days. The other 3 were recaptured 3 weeks later on May 24 near Red Head on the mainland, 20 to 25 miles northeast of the tagging location.

RED HEAD HARBOUR TAGGING

On March 11, 1,965 purse-seined herring were tagged at Lat. $45^{\circ}05'22''$ N, Long. $66^{\circ}35'19''$ W. Forty-four of the 54 recaptures were made within 2 miles of the tagging site and distributed fairly evenly over a 5-week period. No recaptures were made more than 10 miles from the tagging site. Twenty-two recaptures were made at the tagging site. Five recaptures were made eastward in the Pocologan region; 26 westward, chiefly in Seely Cove and Beaver Harbour and 1 at The Wolves Islands.

EAST WOLF ISLAND TAGGING (Fig. 3)

On March 18, 2,966 herring were tagged from a shut-off seine in Southern Cove on East Wolf Island. Out of a total of 143 recaptures, 90 were made at the tagging site—52 from April 7–9; 33 on April 19; 3 on April 24; and 2 on May 8. Forty-eight recaptures were made along the mainland shore from Dipper Harbour to Bliss Island, chiefly within the first 9 weeks, though 2 recaptures were made 18 weeks after tagging. Four recaptures 9 weeks after tagging and 1 recapture 12 weeks after tagging were made at the head of Passamaquoddy Bay.

SEELY COVE TAGGING

On March 20, herring were obtained in Seely Cove from a purse seiner and 1,913 were tagged and released at the mouth of this Cove (Lat. $45^{\circ}05'15''$ N, Long. $66^{\circ}38'15''$ W). Ten recaptures were made; 3 in the first week, 3 in the third, 3 in the fifth, and 1 in the sixth. Only 1 was recaptured within 2 miles of the tagging site, 6 were retaken 2 to 6 miles eastward along the shore and 2 about the same distance westward. One was recaptured offshore at The Wolves Islands about 7 miles away on April 24.

MACES BAY TAGGING

On April 9, herring were obtained in Maces Bay just west of Point Lepreau from a purse seiner and 1,913 were tagged and released at Lat. $45^{\circ}07'10''$ N, Long. $66^{\circ}29'42''$ W. Only 4 tags were recovered, 3 within 2 miles of the tagging site (2 on April 15 and 1 on April 19) and 1 (on May 20) in Bocabec Bay at the head of the Passamaquoddy Bay, 23 miles away.

CROW COVE TAGGING

On April 10, 971 purse-seined herring were tagged and released at Lat. $45^{\circ}06'06''$ N, Long. $66^{\circ}36'44''$ W. The single recovery from this tagging was made on July 7, 13 weeks after tagging, at Mill Cove, Campobello, 15 to 16 miles away.

FOX ISLAND TAGGING (Fig. 4)

On May 2, 2,863 herring were tagged at Fox Island weir. The 43 recaptures were spread over a 12-week period. During the first week 11 recaptures

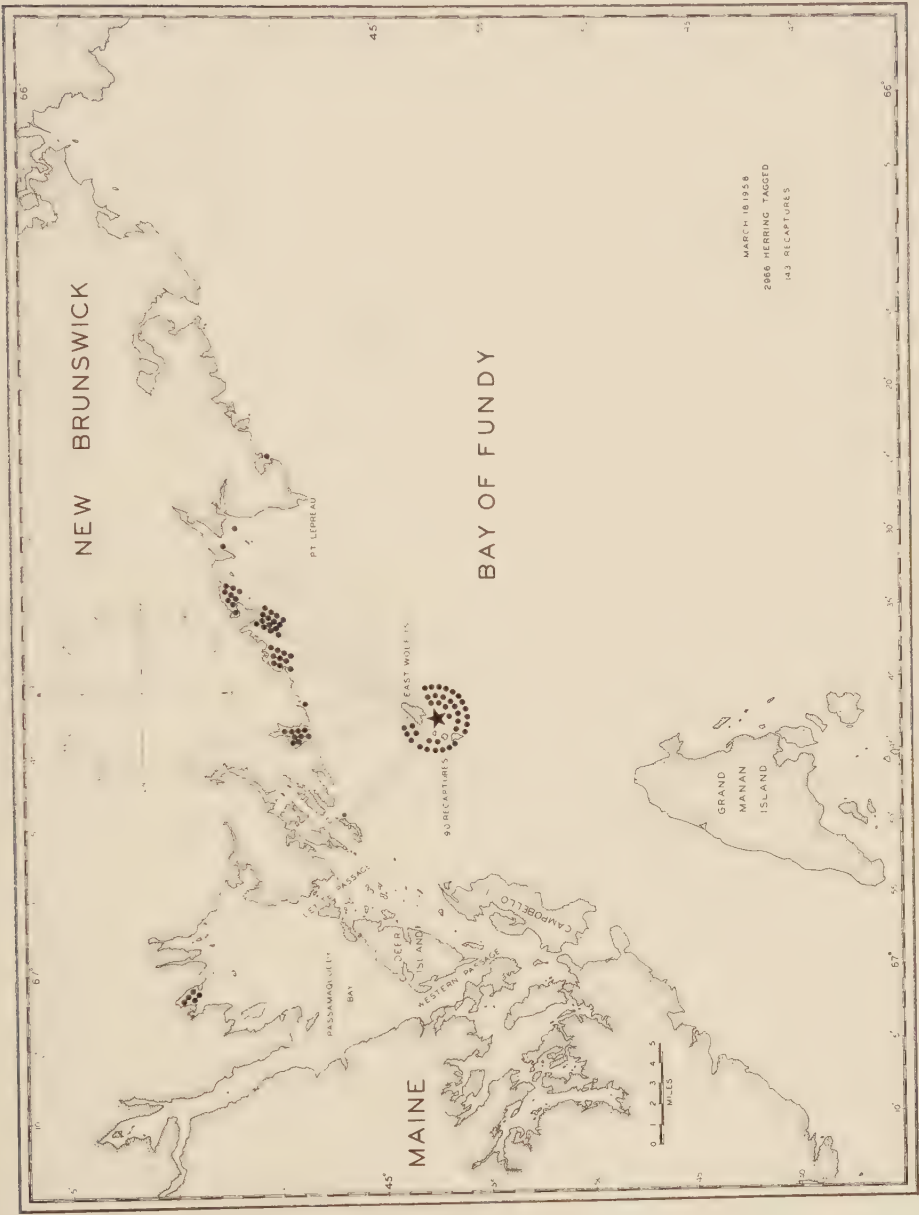


FIG. 3. Recaptures from herring tagged at East Wolf Island, N.B., on March 18, 1958.



FIG. 4. Recaptures from herring tagged at Fox Island, N.B., on May 2, 1958.

were made; 3 in Beaver Harbour, 3 off Seely Head and 5 off Pocologan. There were no recaptures during the second week. During the third week, 4 were retaken at Pocologan and 7 in Bocabec Bay. The recaptures in the fourth to twelfth weeks were made in the same general areas as those made earlier except for 1 at Dipper Harbour and 2 off Campobello. In all, 20 were recaptured eastward to Dipper Harbour, 20 northward in Passamaquoddy Bay, 2 westward to Campobello and 1 at the tagging site.

LORING COVE TAGGING (Fig. 5)

On May 9, 2,970 herring were tagged from George Johnson's weir in Loring Cove. None were recovered in United States waters or within 2 miles of the tagging site. All 234 recaptures were made in a 19-week period following tagging. Most (227) of the recaptures were made at the head of Passamaquoddy Bay. One was recaptured at Seely Cove, 4 near Pocologan, 1 at Mill Cove, Campobello, and 1 off eastern Grand Manan.

BIRCH COVE TAGGING (Fig. 6)

On May 16, 2,974 herring were tagged and released at the Miller weir in Birch Cove. Of the 708 recaptures over 20 weeks, 631 were made within 2 miles of the tagging site and 51 from 2 to 5 miles away. Only 8 recoveries were made outside Passamaquoddy Bay. The others (18) were made near the entrances to the bay and just inside.

HOPE ISLAND TAGGING

On May 16, 2,992 herring were tagged and released off Hope Island, Little Kennebec, Maine, about 25 miles southwest of Passamaquoddy Bay. Of the 41 recaptures, 9 were taken the first week and 32 the second week after tagging. All were recaptured within 2 miles of the tagging site.

MASCARENE SHORE TAGGING (Fig. 7)

On May 22, 2,479 herring were tagged and released from the Mascarene weir on the east side of Passamaquoddy Bay. Recoveries were made over a period of 16 weeks. As at Loring Cove on the west side of Passamaquoddy Bay no recaptures were made within 2 miles of the tagging site. Also, the pattern of recaptures was similar in that 81 of the 91 recaptures were made at the head of Passamaquoddy Bay. Seven recaptures were made in other parts of the bay, 1 outside near the northeast end of Campobello Island and 2 eastward as far as New River Beach.



FIG. 5. Recaptures from herring tagged at Loring Cove, Maine, on May 9, 1958.



Fig. 6. Recaptures from herring tagged at Birch Cove, N.B., on May 16, 1958.



FIG. 7. Recaptures from herring tagged at Mascarene Shore, N.B., on May 22, 1958.

ST. ANDREWS POINT TAGGING

On May 29, 2,956 herring were tagged and released from the Protection weir. Of the 144 recoveries in 24 weeks 127 were made at the head of Passamaquoddy Bay. Four recaptures were made at the tagging site, 10 among the islands at the mouth of this bay, and 3 near Pocologan. In general, recoveries were similar to those for the Loring Cove and Mascarene Shore taggings.

NEW RIVER ISLAND TAGGING

On June 4, 1,937 herring were tagged and released from the Bartlett weir off New River Island just west of Point Lepreau. Fourteen recaptures were made over an 8-week period. Eleven of these were recovered within 2 miles of the tagging site, 1 near Saint John about 20 miles eastward, and 2 about 20 miles westward—1 in Bocabec Bay and the other in Mill Cove, Campobello.

BEAN ISLAND TAGGING

On June 10, 1,889 herring were tagged and released from the Giller weir off Bean Island. Sixty-seven recaptures were made over a 21-week period following tagging. Here again most (47) of the tagged fish were taken at the head of Passamaquoddy Bay. Six recaptures were made at other points in the bay, 2 were recaptured at the tagging site and 12 along the shore eastward towards Point Lepreau.

MILL COVE, CAMPOBELLO, TAGGING

On June 17, 1,399 herring were tagged and released from the Mill Cove weir on the eastern end of Campobello Island. Of the 180 recaptures within 12 weeks, 163 were made at the tagging site. Of the other 17 recaptures, 10 were made at various locations in the Passamaquoddy region, 6 eastward as far as Saint John and 1 off Digby Neck, Nova Scotia.

MOOSE RIVER COVE TAGGING (Fig. 8)

On June 17, 2,959 herring were tagged and released in the outer part of Moose River Cove about 8 miles west of West Quoddy Head. There were 30 recaptures altogether, 29 within 7 weeks and 1 during the twelfth week. One recapture was made at the tagging site and 1 just east of it. Westward there were 16 recaptures at Cutler, Maine, and 1 at Jonesport, Maine. Eastward there was 1 at Grand Manan, 2 in Passamaquoddy Bay and 8 along the New Brunswick shore from Letite Passage to Dipper Harbour.

BEAN ISLAND TAGGING

On June 9, 2,960 herring were tagged and released from the Giller weir located off Bean Island. Of the 112 recaptures over 21 weeks, only 17 were made at the tagging site. Most (82) of the recaptures were made in Passamaquoddy Bay. Of the remainder, 1 was retaken off the western end of Deer Island, 2 in Mill Cove, Campobello, and 10 along the shore from Letite to Musquash Harbour, just west of Saint John.

GRIFFINS COVE TAGGING

On June 24, 2,405 herring were tagged and released from the Sidney Westcott weir, Digby Neck, N.S. Only 3 recaptures were ever recorded from this tagging, 2 at the tagging site during the first week after tagging and 1 off Deer Island during the second week.

SPIDER COVE TAGGING

On July 2, 2,984 herring were tagged and released from the Trial weir in Spider Cove, Bliss Island. The majority (319) of the 335 recaptures were made within 3 weeks of tagging, most (270) of them at the tagging site. The remaining 65 were retaken away from the tagging location in various directions, 49 eastward as far as Dipper Harbour, 9 southwestward to Mill Cove, Campobello, 6 north-westward to the head of Passamaquoddy Bay, and 1 northeastward into the Letang River estuary. No recoveries were made after the thirteenth week.

ST. ANDREWS POINT TAGGING

On July 3, 2,945 herring were tagged and released from the Short Bar weir off St. Andrews Point. In general, the fish moved either northeastward towards the head of Passamaquoddy Bay (21 recoveries) or out of the bay eastward along the New Brunswick shore (7 recoveries). Three recaptures were made at other points in Passamaquoddy Bay. All recaptures were made within 10 weeks.

BOCABEC BAY TAGGING

On July 4, 2,993 herring were tagged and released from the Orr weir at the head of Bocabec or Big Bay. Of the 112 recaptures 102 were made in the first 4 weeks after tagging and 10 in the following 15 weeks. Eighty-nine recaptures were made close to the tagging site, 20 near the eastern entrance to Passamaquoddy Bay, 2 near the western entrance to this bay, and 1 near Point Lepreau.

SPRUCEHEAD ISLAND TAGGING

On July 9, 1,970 herring were tagged and released from the Harold Simmons' weir off Rockland, Maine. Only 1 recapture was ever recorded and that from the Simmon's weir on July 21.

EAST BAY TAGGING

On July 10, 2,976 herring were tagged and released from the Tucker-Parker stop seine in Cobscook Bay, Maine. Sixty of the 63 recaptures were made within 3 weeks of tagging, and all within 9 weeks. Fifty-six recaptures were made near the tagging site, 1 at Little Machias Bay, 4 in other parts of Cobscook Bay, and 2 in Passamaquoddy Bay.

GREAT CHEBEAGUE ISLAND TAGGING

On July 11, 2,104 herring were tagged and released from Henry Dyer's stop seine off Great Chebeague Island, Casco Bay, near Portland, Maine. Only 1 was ever recorded as recaptured and that on July 16 at Little John Island off Yarmouth, Maine, about 2 to 3 miles from the tagging site.

LINEKIN BAY TAGGING

On July 17, 2,933 herring were tagged and released from Brink Chapman's stop seine at the head of Linekin Bay, Boothbay Harbor, Maine. There was only 1 recorded recapture and that on July 21 in Linekin Bay.

ST. ANDREWS POINT TAGGING

On July 25, 2,918 herring were tagged and released from the Navy Island weir. No recaptures were recorded during the first 3 weeks following tagging. There were 19 recaptures altogether, 14 of them within Passamaquoddy Bay. In addition, there was 1 recapture near the eastern and 2 near the western entrances to the bay, and 1 at Musquash near Saint John. The final record for this tagging was a recapture in the fifteenth week on the Nova Scotia side of the Bay of Fundy.

DIPPER HARBOUR TAGGING (Fig. 9)

On July 31, 2,959 herring were tagged and released from the Plumper weir at the entrance to Dipper Harbour. During the first week 15 of the 19 recaptures were recorded, 14 in Sand Cove near Saint John about 18 miles east of the tagging site, and 1 off Lorneville about 13 miles eastward. From 2 to 5 weeks later, 3 were recaptured in Musquash Harbour and 1 in Sand Cove. No recoveries were made at the tagging site. All were made eastward towards Saint John. Fourteen of the tagged fish moved about 18 miles in 4 days.

NEW RIVER BEACH TAGGING (Fig. 9)

On August 1, 2,970 herring were tagged and released from the Harvester weir at New River Beach. In the first week after tagging, 53 of the total of 59 recaptures were recorded, all within 2 miles of the tagging site. Two more were recaptured in the second and third weeks, both from the tagging area. During the sixth week, 3 were recovered at the head of Passamaquoddy Bay, almost 20

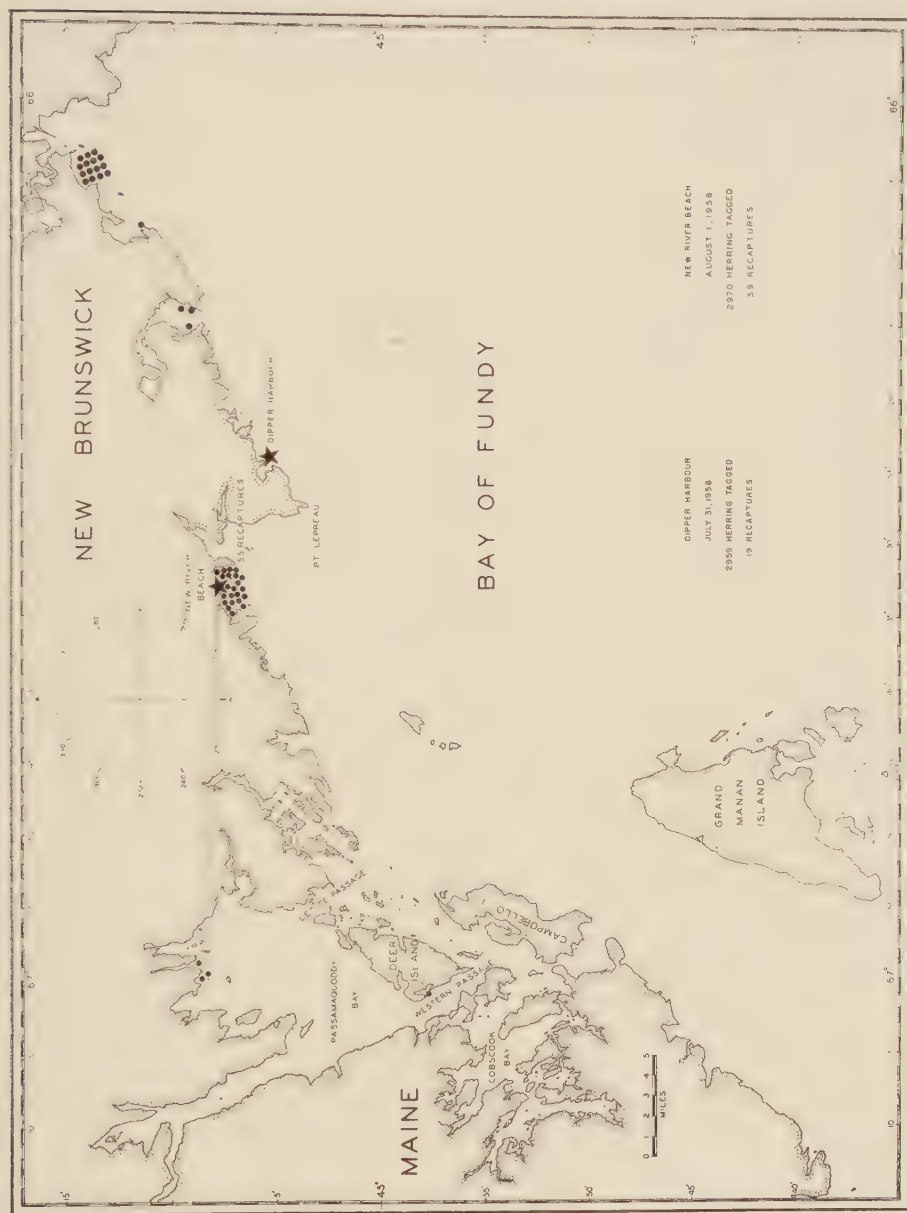


FIG. 9. Recaptures from herring tagged at Dipper Harbour, N.B., on July 31, 1958; New River Beach, N.B., on August 1, 1958.

miles in a straight line westward. The final recapture was made off Fairhaven at the west end of Deer Island on November 10, 15 weeks after tagging.

The majority of the recaptures were made near the tagging site. However, some were made to the westward, as shown by the recaptures at the head of Passamaquoddy Bay and off western Deer Island. This movement is in the opposite direction to that indicated by the Dipper Harbour tagging on the previous day.

EAGLE ISLAND TAGGING

On August 6, 1,472 herring were tagged and released from the Eagle Island weir just outside and to the east of Letite Passage. Only 2 recaptures were recorded, 1 in the first week about a mile away from the tagging site and 1 six weeks after tagging at the head of Passamaquoddy Bay.

SEELY COVE TAGGING

On August 20, 2,531 herring were tagged and released from the Comet weir at the western entrance to Seely Cove. Of the 11 recaptures, 4 were made west (as far as Passamaquoddy Bay) of the tagging site, and 7 east (as far as Musquash Harbour) of it. In this tagging, unlike that at either Dipper Harbour or New River Beach, recaptures were made nearly 20 miles away both westward and eastward and all within 4 weeks.

SPRUCEHEAD ISLAND TAGGING

On August 20, 2,949 herring were tagged and released from the Edgar Post weir off Sprucehead Island, Maine. On August 26, the single recapture from this tagging was made within 2 miles of the tagging site.

GLEASON COVE TAGGING

On August 26, 2,623 herring were tagged and released from Edwin Evan's weir in Gleason Cove, Maine. There were 44 recaptures within 5 weeks, 1 at the tagging site, 5 along the Maine shore inside Passamaquoddy Bay, 5 off the north side of Deer Island, and 33 at the head of Passamaquoddy Bay.

MCCANN COVE TAGGING

On August 29, 2,951 herring were tagged and released from the McCann Cove weir. All 24 recaptures were made inside Passamaquoddy Bay within 6 weeks after tagging.

HOLT POINT TAGGING

On September 4, 1,494 herring were tagged and released from the Holt Point weir. All 23 recaptures were made at the head of Passamaquoddy Bay, 12 in the first week after tagging and 11 during the second week.

PASSAMAQUODDY BAY TAGGING

On September 5, 2,982 herring were tagged and released from purse-seine catches at Lat. 45°02'45"N, Long. 66°59'30"W in the deeper, open waters of Passamaquoddy Bay, about 1½ miles northwest of Pendleton Island. There were 50 recaptures, 23 within the first week after tagging and the remainder during the following 3 weeks. Some (22) of these fish were retaken by weirs northeastward towards the head of the bay. The remainder (28) were retaken by purse seiners in the deeper waters of the bay.

TWO ISLAND HARBOUR TAGGING

On September 24, 1,460 herring were tagged and released from the Good Luck weir, Two Island Harbour, Grand Manan. Three recaptures were made, 1 in the first week after tagging, another in the second week (both within 2 miles of the tagging site) and the third during the sixth week at Pats Cove about 3 miles away.

LOBSTER COVE TAGGING

On October 15, 2,169 herring were tagged and released from Bradley's stop seine in Lobster Cove, Boothbay Harbor, Maine. The 2 recaptures were made in Linekin Bay, Boothbay Harbor, 5 days later.

CAPITOL ISLAND TAGGING

On October 17, 2,935 herring were tagged and released from Swett's stop seine at Capitol Island, Boothbay Harbor, Maine. The single recapture was made 3 days later in Linekin Bay, Boothbay Harbor.

ADDITIONAL TAGGINGS

No recaptures were recorded from 1,126 herring tagged at Sandy Cove, Digby Neck, N.S., on June 25; from 1,480 herring tagged at Chandler Bay, Maine, on July 8; from 2,128 herring tagged at Cedar and Laireys Island, Maine, on August 19; and from 1,460 herring tagged at Long Pond Bay on September 23.

DRIFT BOTTLE AND TAG RECOVERIES

During 35 of the tagging experiments in 1958, a total of 1,725 drift bottles were released at the same time as the tagged fish to discover whether there was a relationship between herring movements and the drift of surface waters. Usually 48 drift bottles were released during each tagging. Bottle recoveries varied from 4.2 to 89.7% with an overall average of 31.5% (Table III).

In some cases, the tagged herring and the drift bottles moved in the same direction; in other cases, they moved in the opposite direction. In many instances, there was no apparent relationship between the direction of the tagged fish and bottle movements.

TABLE III. Drift bottle releases and recoveries, 1958.

Location	Date	Releases	Recoveries	
			no.	%
Red Head Harbour, N.B.	Mar. 11	48	14	29.2
East Wolf Island, N.B.	Mar. 18	48	17	35.4
Seely Cove, N.B.	Mar. 20	48	6	12.5
Maces Bay, N.B.	Apr. 9	48	8	16.7
Crow Cove, N.B.	Apr. 10	48	5	10.4
Fox Island, N.B.	May 2	48	18	37.6
Loring Cove, Me.	May 9	48	19	39.6
Hope Island, Me.	May 16	48	16	33.3
Birch Cove, N.B.	May 16	48	43	89.7
Mascarene Shore, N.B.	May 22	48	14	29.2
St. Andrews Point, N.B.	May 29	48	13	27.0
New River Island, N.B.	June 4	48	16	33.3
Bean Island, N.B.	June 10	48	11	22.9
Mill Cove, N.B.	June 17	48	9	18.7
Moose River Cove, Me.	June 17	48	5	10.4
Bean Island, N.B.	June 19	48	17	37.5
Griffin Cove, N.S.	June 24	48	15	31.3
Sandy Cove, N.S.	June 25	48	2	4.2
Spider Cove, N.B.	July 2	48	14	29.2
St. Andrews Point, N.B.	July 3	48	24	50.0
Bocabec Bay, N.B.	July 4	48	38	79.2
Chandler Bay, Me.	July 8	48	6	12.5
East Bay, Me.	July 10	48	23	48.0
Navy Island, N.B.	July 25	48	15	31.3
Dipper Harbour, N.B.	July 31	44	6	13.4
New River Beach, N.B.	Aug. 1	48	8	16.7
Eagle Island, N.B.	Aug. 6	48	22	45.9
Cedar and Laireys, Is., Me.	Aug. 19	48	7	14.6
Sprucehead Island, Me.	Aug. 20	48	34	70.8
Seely Cove, N.B.	Aug. 20	48	8	16.7
Gleason Cove, Me.	Aug. 26	48	15	31.3
McCann Cove, N.B.	Aug. 29	48	34	69.5
Holt Point, N.B.	Sept. 4	48	8	16.7
Passamaquoddy Bay, N.B.	Sept. 5-6	49	20	40.8
Long Pond Bay, N.B.	Sept. 23	48	4	8.3
Two Island Harbour, N.B.	Sept. 24	48	9	18.7
Total		1,725	543	31.5

DISCUSSION AND CONCLUSIONS

The purpose of the tagging experiments was to determine the pattern of movement of herring in the Passamaquoddy area and hence to provide information that would assist in predicting the effects that the proposed tidal power project (Hart and McKernan, 1960) might have on the herring fisheries in the area. Taggings were done during the commercial fishing season and it is believed that the movements of tagged fish are indicative of the movements of herring supporting the fishery.

No comparisons of the amount of movement in different directions was possible because exact information on the amount of fishing effort was not available. However, the number of weirs fished in an area varies little within a season and the variation in the number of tags recovered in a particular locality may well indicate differences in the amount of movement there.

Distance, duration and direction of movements of herring tagged in 1958 are discussed below and comparisons are made with the results of the 1957 taggings. Recoveries of tagged fish in 1958 varied from 0 to 24.0% (Table I) as contrasted with 0 to 12.7% in 1957 (McKenzie and Skud, 1958). Only scarlet tags were used in 1957 whereas in 1958 scarlet, maroon and yellow tags were used. However differences for the various colours were not related to the extent or direction of movement nor the length of time between tagging and recapture. The only detectable difference was that the percentage recovery was considerably higher for scarlet tags (4.5%) than for maroon (2.2%) or yellow (0.2%) tags.

DISTANCES MOVED

Analyses of movements of fish are based chiefly on recaptures made more than 2 miles from the points of release. These include 1,179 recaptures or nearly 44% (approximately 47% in 1957) of the total recaptures from 1958 taggings.

Table IV shows that more than 6% of the recaptures in 1958 were made within 2 to 5 miles and over 25% within 5 to 10 miles of the points of release. At greater distances, recaptures declined sharply. The greatest distance moved was 55 miles. Except for minor variations in percentage recoveries results were the same for 1957 (Table V). Some herring travelled long distances within short periods. The average minimum rate of movement for tagged herring that moved from 20 to 55 miles was 1.0 mile per day with a range of 0.2 to 11.3 miles per day. Recovery data did not show the amount of wandering between points of release and recapture. However it is interesting, and perhaps significant, that the maximum rate of movement (11.3 miles per day) is very similar to calculated speeds (10 miles per day) for non-tidal surface currents in the area (Trites, 1959).

TABLE IV. Recaptures of tagged herring at various distances from points of release (1958).

Taggings	Distance in miles					Total
	0-2	2-5	5-10	10-25	25-55	
Long Island Bay, N.B.	4	0	0	3	...	7
Red Head Harbour, N.B.	44	0	10	...	...	54
East Wolf Island, N.B.	90	0	36	17	...	143
Seely Cove, N.B.	1	7	2	...	...	10
Maces Bay, N.B.	3	0	0	1	...	4
Crow Cove, N.B.	0	0	0	1	...	1
Fox Island, N.B.	1	3	8	31	...	43
Loring Cove, Me.	0	1	227	6	...	234
Birch Cove, N.B.	631	51	11	15	...	708
Hope Island, Me.	41	...	...	...	...	41
Mascarene Shore, N.B.	0	2	88	1	...	91
St. Andrews Point, N.B.	4	20	117	3	...	144
New River Island, N.B.	11	0	0	3	...	14
Bean Island, N.B.	2	7	15	43	...	67
Mill Cove, N.B.	163	2	8	4	3	180
Moose River Cove, Me.	1	1	16	6	6	30
Bean Island, N.B.	17	11	31	52	1	112
Griffin Cove, N.S.	2	0	0	0	1	3
Spider Cove, N.B.	270	1	23	41	...	335
St. Andrews Point, N.B.	2	5	23	1	...	31
Bocabec Bay, N.B.	74	12	3	23	...	112
Sprucehead Island, Me.	1	...	...	...	...	1
East Bay, Me.	56	2	2	3	...	63
Great Chebeague Is., Me.	1	...	...	...	...	1
Linekin Bay, Me.	1	...	...	...	...	1
Navy Island, N.B.	0	4	13	0	2	19
Dipper Harbour, N.B.	0	0	3	16	...	19
New River Beach, N.B.	55	0	0	4	...	59
Eagle Island, N.B.	1	0	0	1	...	2
Seely Cove, N.B.	0	1	7	3	...	11
Sprucehead Island, Me.	1	...	...	...	...	1
Gleason Cove, Me.	4	5	3	32	...	44
McCann Cove, N.B.	3	18	3	...	...	24
Holt Point, N.B.	20	3	...	...	...	23
Passamaquoddy Bay, N.B.	0	16	34	...	...	50
Two Island Harbour, N.B.	2	1	...	...	...	3
Lobster Cove, Me.	2	...	...	...	...	2
Capitol Island, Me.	1	...	...	...	...	1
Totals	1,509	173	683	310	13	2,688
Percentage	56.1	6.4	25.4	11.6	.3	100

TABLE V. Recaptures of tagged herring at various distances from points of release (1957).

Taggings	Distance in miles					Total
	0-2	2-5	5-10	10-25	25-55	
Moat Island, N.B.	1	3	7	0	2	13
Harbour de Loutre, N.B.	12	0	3	8	0	23
Bocabec, N.B.	101	7	2	12	6	128
New River Beach, N.B.	20	10	7	11	0	48
Pats Cove, N.B.	7	0	8	4	14	33
Lords Cove, N.B.	13	0	24	2	...	39
Frost Cove, Me.	0	18	4	9	1	32
McDougal's Island, N.B.	29	13	13	6	...	61
Bucks Harbor, Me.	1	0	0	0	1	2
Johnson Bay, Me.	47	0	6	6	1	60
Bocabec, N.B.	3	0	...	...	...	3
Cumberland Shore, N.B.	0	0	0	0	2	2
Totals	234	51	74	58	27	444
Percentage	52.7	11.5	16.6	13.1	6.1	100

TIME AT LARGE

There was considerable variation in the length of time between tagging and recapture. In 1958, 24.4% of the recaptures were made during the first week, 36.5% during the second week, and 18.8% during the third week (Table VI). The remainder (20.3%) were spread over a period of 4 to 24 weeks after tagging. The average time between release and recapture was 17 days but the variation was from a few hours to 165 days. In both 1957 and 1958 more than 90% of the recaptures were made within the first 5 weeks. However, in 1957 all recaptures were made within 12 weeks (Table VII), the maximum time at large being 82 days.

In general, for both 1957 and 1958, the numbers of tagged fish retaken near the tagging site (0 to 2 miles) declined with time while those retaken farther away (2 to 55 miles) increased (Table VIII).

Table IX gives the time lapse between release and recapture for long distance (20 to 55 miles) travellers for 1957 and 1958 taggings combined. There is no apparent order in the average number of days taken to travel various distances and the conclusion must be that a great deal of wandering takes place.

DIRECTION OF MOVEMENT

Almost half of the recaptures from the 1957 and 1958 taggings were made more than 2 miles away from the tagging sites (Table VIII). The pattern of distant recaptures indicated that herring movements were usually in more than one direction with no regular seasonal differences in direction.

TABLE VI. Recaptures of tagged herring at weekly intervals following tagging (1958).

Taggings	Time to recapture									Total
	1st	2nd	3rd	4th	5th	6th	7th	8th	9-24th	
Long Island Bay, N.B.	4	0	3	...	...	...	...	...	...	7
Red Head Harbour, N.B.	11	5	13	5	9	2	1	0	8	54
East Wolf Island, N.B.	16	5	9	53	35	9	3	5	8	143
Seely Cove, N.B.	3	0	3	0	3	1	...	...	...	10
Maces Bay, N.B.	2	1	0	0	0	1	...	...	...	4
Crow Cove, N.B.	0	0	0	0	0	0	0	0	1	1
Fox Island, N.B.	11	0	11	8	4	2	0	0	7	43
Loring Cove, Me.	5	64	136	13	9	0	2	1	4	234
Birch Cove, N.B.	170	399	35	31	5	19	5	6	38	708
Hope Island, Me.	9	32	...	...	...	...	...	...	...	41
Mascarene Shore, N.B.	46	18	9	1	0	6	2	1	8	91
St. Andrews Point, N.B.	56	51	3	2	12	6	5	0	9	144
New River Island, N.B.	2	0	3	3	0	3	2	1	...	14
Bean Island, N.B.	0	2	32	10	8	4	3	3	5	67
Mill Cove, N.B.	54	2	103	10	9	1	0	0	1	180
Moose River Cove, Me.	0	3	2	2	4	17	1	0	1	30
Bean Island, N.B.	23	48	9	14	8	3	4	0	3	112
Griffin Cove, N.S.	2	1	...	...	...	...	...	...	...	3
Spider Cove, N.B.	71	171	77	8	6	0	1	0	1	335
St. Andrews Point, N.B.	7	12	6	2	0	1	1	1	1	31
Bocabec Bay, N.B.	24	63	7	8	0	0	0	6	4	112
Sprucehead Island, Me.	0	1	...	...	...	...	...	...	...	1
East Bay, Me.	11	29	20	1	0	1	0	0	1	63
Great Chebeague Is., Me.	1	...	...	...	...	...	...	...	...	1
Linekin Bay, Me.	1	...	...	...	...	...	...	...	...	1
Navy Island, N.B.	0	0	0	3	2	1	7	1	5	19
Dipper Harbour, N.B.	15	1	1	0	2	...	...	...	...	19
New River Beach, N.B.	53	1	1	0	0	3	0	0	1	59
Eagle Island, N.B.	1	0	0	0	0	1	...	...	...	2
Seely Cove, N.B.	6	2	2	1	...	...	...	...	...	11
Sprucehead Island, Me.	1	...	...	...	...	...	...	...	...	1
Gleason Cove, Me.	7	21	14	1	1	...	...	...	...	44
McCann Cove, N.B.	4	16	3	0	0	1	...	...	...	24
Holt Point, N.B.	12	11	...	...	...	...	...	...	...	23
Passamaquoddy Bay, N.B.	23	22	2	3	...	...	...	...	...	50
Two Island Harbour, N.B.	1	1	0	0	0	1	...	...	...	3
Lobster Cove, N.B.	2	...	...	...	...	...	...	...	...	2
Capitol Island, Me.	1	...	...	...	...	...	...	...	...	1
Totals	655	982	504	179	117	83	37	25	103	2,688
Percentage	24.4	36.5	18.8	6.7	4.4	3.1	1.4	.9	3.8	100

TABLE VII. Recaptures of tagged herring at weekly intervals following tagging (1957).

Taggings	Time to recapture									Total
	1st	2nd	3rd	4th	5th	6th	7th	8th	9-12th	
Moat Island, N.B.	0	1	5	4	1	0	0	0	2	13
Harbour de Loutre, N.B.	8	6	6	3	...	...	...	...	...	23
Bocabec, N.B.	72	40	12	0	2	1	1	...	...	128
New River Beach, N.B.	26	12	4	4	0	0	0	0	2	48
Pats Cove, N.B.	14	10	2	3	2	0	0	0	2	33
Lords Cove, N.B.	14	15	1	4	0	1	3	1	...	39
Frost Cove, Me.	11	15	4	1	0	1	...	...	...	32
McDougal's Island, N.B.	34	14	3	10	...	...	...	...	...	61
Buck's Harbor, Me.	0	1	1	...	...	...	...	...	...	2
Johnson Bay, Me.	48	2	5	5	...	...	...	...	...	60
Bocabec, N.B.	3	...	...	...	...	...	...	...	...	3
Cumberland Shore, N.B.	2	...	...	...	...	...	...	...	...	2
Totals	232	116	43	34	5	3	4	1	6	444
Percentage	52.2	26.1	9.7	7.7	1.1	0.7	9.9	0.2	1.4	100

TABLE VIII. Percentage recaptures of herring within and outside tagging areas by weekly periods 1957 and 1958.

Weekly periods	1957		1958	
	within (0-2 miles)	outside (2-55 miles)	within (0-2 miles)	outside (2-55 miles)
	%	%	%	%
1st	69	31	65	35
2nd	47	53	67	33
3rd	19	81	41	59
4th	35	65	60	40
5th	0	100	45	55
6th	0	100	28	72
7th	0	100	19	81
8th	0	100	40	60
9th-24th	0	100	15	85
Average	53	47	56	44

TABLE IX. Time lapse between release and recapture of tagged herring that moved 20 to 55 miles (1957 and 1958 taggings).

Distance (miles)	No. of fish	Days from release to recapture		
		Min.	Max.	Av.
20-25	48	2	101	32
25-30	15	6	60	20
30-35	11	7	69	22
35-40	8	4	63	26
40-45	3	16	34	26
45-55	3	9	102	43

EAST OF PASSAMAQUODDY BAY. Herring tagged east of Passamaquoddy Bay in both 1957 and 1958 were recaptured chiefly near the tagging site following the general recovery pattern. However, taggings in March and April 1958 showed that there was some movement westward to Passamaquoddy Bay. No tagging was done east of the bay in May. From the one June tagging (1958) there were recaptures both westward to Passamaquoddy Bay and eastward to Saint John. July and August taggings showed a complex recapture pattern. In July 1957 recaptures from a tagging at New River Beach indicated a pronounced movement westward to Passamaquoddy Bay. A tagging in July 1958 showed an equally well pronounced movement eastward towards Point Lepreau although a few recaptures were made in the bay itself. Another tagging in July 1958 showed eastward movement only as no recaptures were made either locally or westward (Fig. 9). From a tagging at New River Beach on August 1, 1958, there were only 4 distant recaptures, all westward in Passamaquoddy Bay (Fig. 9). From a tagging 3 weeks later (August 20, 1958) at Seely Cove, about 5 miles from New River Beach, recoveries were made from both directions; eastward nearly to Saint John and westward to Passamaquoddy Bay. There were no taggings east of the bay in September. The only autumn tagging east of this bay (Cumberland Shore, October 2, 1957) gave 2 recaptures both about 25 miles eastward towards Saint John.

Altogether there were 12 taggings done east of Passamaquoddy Bay from March to October, 2 in 1957 and 10 in 1958. The recoveries as a whole indicated that during most of the year herring moved randomly in two directions along the shore; westward as far as the bay and eastward as far as Saint John.

SOUTH OF PASSAMAQUODDY BAY. Taggings south of Passamaquoddy Bay were carried out at The Wolves Islands, at Grand Manan, and on the Nova Scotia side of the Bay of Fundy. The tagging at The Wolves (East Wolf Island) was done on March 18, 1958 (Fig. 3). There were 5 taggings at Grand Manan, 1 in August and 1 in November, 1957, 1 in March and 2 in September, 1958. The pattern of recapture from the tagging at The Wolves indicated that a body of herring lay offshore there during most of April and early May but moved inshore at irregular intervals where they were caught with shut-off seines. All of the local recaptures (90) were made from catches on April 7, 19, 24 and May 8, and these were the only 4 commercial catches made at The Wolves during this period.

Distant recaptures (53) from The Wolves tagging were made chiefly north-eastward along the shore from Beaver Harbour to Maces Bay although 5 were recaptured in Passamaquoddy Bay. In contrast to the recovery pattern at the tagging site, the distant recaptures were spread out over a period of 4 months (March 24 to July 18), at least 25 separate catches were involved and with one possible exception, not more than 3 tags were recovered from any single catch.

From two of the taggings at Grand Manan (White Head, November 1957

and Long Pond Bay, September 1958) there were no recoveries. From a tagging at Two Island Harbour (September 1958) there were 3 recaptures, all at the tagging site. From a tagging at Long Island Bay (March 1958) there were 7 recaptures, 4 in the tagging area and 3 northeastward in Maces Bay.

The most informative Grand Manan tagging was done at Pats Cove in August 1957 (Fig. 10). Recaptures showed two distinct movements; one westward to the coast of Maine and the other northward to Passamaquoddy Bay. The recaptures on the coast of Maine were made at Jonesport and Cape Split from 35 to 40 miles from the tagging site. Of the 15 recaptures in the bay area, 8 were made near the eastern entrance (Letite Passage) to the bay and the other 7 at the head of the bay.

Although conclusions are based chiefly on only 2 taggings (East Wolf Island and Pats Cove) there is a suggestion of a rather pronounced movement of herring from the offshore areas of The Wolves and Grand Manan towards Passamaquoddy Bay and the area between the bay and Point Lepreau. The recaptures at Jonesport and Cape Split suggest a slight movement from Grand Manan westward to the coast of Maine.

From taggings on the Nova Scotia side of the Bay of Fundy only 1 (from Griffin Cove tagging, June 24, 1958) of the 8,467 herring tagged is known to have crossed to the Passamaquoddy area. Only 2 are known to have crossed in the opposite direction, 1 from the Mill Cove, Campobello tagging on June 17, 1958, and 1 from the Navy Island tagging on July 25, 1958.

WEST OF PASSAMAQUODDY BAY. There were 13 taggings westward of Passamaquoddy Bay, 3 in 1957 and 10 in 1958. From all but 2 taggings, recoveries were mainly local providing little information on herring movements. From a tagging (September 1957) at Buck's Harbor, Maine, about 25 miles westward of the bay, there were only 2 recaptures, 1 local and the other about 50 miles to the eastward near Point Lepreau (McKenzie and Skud, 1958). There were 30 recoveries from a tagging (June 1958) at Moose River Cove, Maine, about 10 miles west of Passamaquoddy Bay (Fig. 8). Two recaptures were made near the tagging site, 17 westward (10 to 15 miles) along the coast of Maine, 1 south-eastward (12 to 15 miles) to Grand Manan, 8 northeastward (20 to 40 miles) along the shore between Letite Passage and Dipper Harbour, and 2 inside Passamaquoddy Bay. The results indicate some movement of herring from the east part of the coast of Maine to the Passamaquoddy area and farther east but none from the more westerly Maine shore. This suggests differences in the herring from eastern and western Maine waters and is in agreement with the conclusions reached by Sindermann (1957a and b) and Sindermann and Mairs (1959) that there is a difference in the herring stocks east and west of Mount Desert Island.

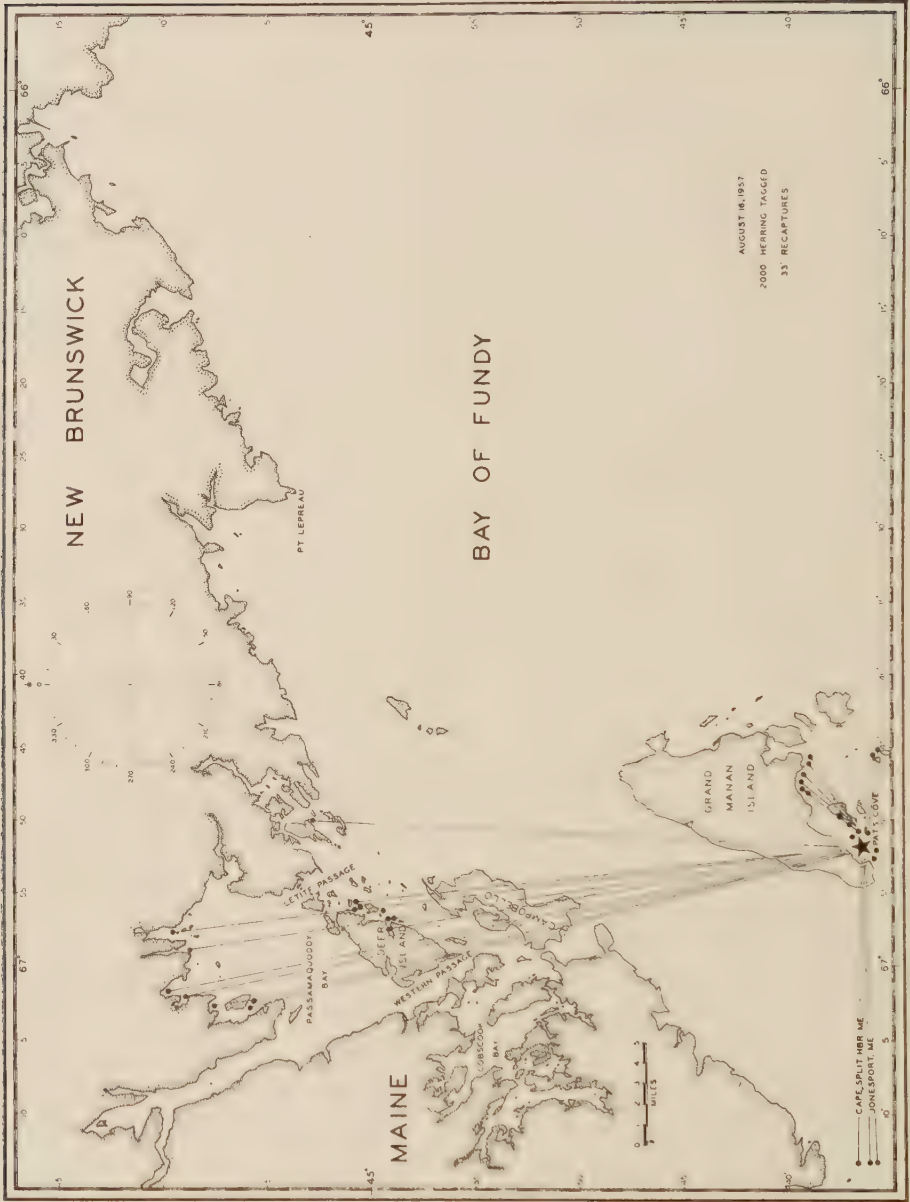


Fig. 10. Recaptures from herring tagged at Pats Cove, N.B., on August 16, 1957.

ENTRANCES TO PASSAMAQUODDY BAY. Tagging among the islands at the mouth of Passamaquoddy Bay in both 1957 and 1958 showed that in May almost half of the tagged herring moved rapidly into the bay while the other half moved eastward towards Point Lepreau (Fig. 4). From June taggings 56.5% of the recaptures were made near the tagging sites, 38.2% inside the bay, and 5.3% to the eastward (Fig. 11). From July taggings 83.6% of the recaptures were made near the tagging site, 14.6% to the eastward, and 1.8% inside Passamaquoddy Bay. Most (95%) of the recaptures from August taggings were made among the islands or within the bay, none eastward. There was no tagging done in September in this area. Almost all (99%) of the recaptures from October taggings were made either near the tagging sites (93%) or inside Passamaquoddy (6%).

Recaptures in the passages were few, possibly because there are not many weirs in these areas. However, the few recoveries indicated that most entries and exits were via Letite Passage rather than Western Passage.

INSIDE PASSAMAQUODDY BAY. Most recoveries from taggings inside Passamaquoddy Bay were made within the bay, some were made among the islands at the mouth of the bay and some about 27 miles eastward along the shore as far as Musquash. There is only 1 record (questionable) of a recapture made to the westward along the coast of Maine.

Taggings in the outer half of Passamaquoddy Bay demonstrated a movement to the head of the bay (e.g., Loring Cove, May 9, 1958, Fig. 5, and Mascarene Shore, May 22, 1958, Fig. 7) while taggings at the head of the Bay showed most of the recaptures at the tagging site, (e.g., Birch Cove, May 16, 1958, Fig. 6). However, the taggings in both parts of Passamaquoddy Bay yielded about the same proportion of recaptures outside the bay. The earliest taggings in the bay were carried out in May (11,379 herring tagged) and of the 1,177 recaptures, 96.9% were retaken inside and 3.1% among the islands at the mouth and farther away—usually eastward. No taggings were carried out in Passamaquoddy Bay in June. In July of the two years 11,830 herring were tagged and 290 were recaptured—17.6% from among the islands at the mouth of the bay or eastward. All the recaptures from August taggings (5,574 fish tagged) in Passamaquoddy Bay were made inside the bay. In September, 166 of the 10,461 tagged fish were recaptured and of these, 7.2% were recaptured outside the bay. The October taggings of 2,963 herring yielded only 3 recaptures, all within Passamaquoddy Bay. These taggings thus showed that many fish moved out of the bay during the season and that in July, especially in 1958, this movement reached its peak.

COBSCOOK BAY. On the whole taggings showed much less movement in and out of Cobscook Bay than Passamaquoddy Bay. Of the 57 taggings carried out in 1957 and 1958 outside of Cobscook Bay only 2 yielded any recaptures within this bay—1 from the Frost Cove tagging in 1957 and 1 from the Mill Cove tagging in 1958. Although the average annual catch of herring (1947 to 1958) in Passamaquoddy Bay (McKenzie and Tibbo, 1960) is nearly 6 times greater than in Cobscook Bay (Scattergood and Lozier, 1959), tag recoveries in Passamaquoddy Bay from releases outside were more than 100 times those in Cobscook Bay.



FIG. 11. Recaptures from herring tagged at Harbour de Loutre, N.B., on June 21, 1957.

RECAPITULATION. The overall results of the tagging experiments in 1957 and 1958 showed that, during the spring and early summer (March to June), the movement of herring was, in general, into Passamaquoddy Bay and along the shore eastward almost to Saint John. In July the inward movement continued but there appeared to be a greater movement outwards and to the eastward. The inward movement continued in August but the outward movement declined. Tagging in September and October showed much less movement in all directions than at other times of year.

The variations in recaptures in the different regions occurred in spite of the fact that there is little change in the number of weirs fishing until late in October or early November. The Charlotte County herring fishery is at its peak in August outside of Passamaquoddy Bay and in September inside the bay (McKenzie and Tibbo, 1960). With 80 to 90% of the tags being recovered within a month of release there was adequate time for tags to be recovered (from taggings prior to mid-September) before any of the weirs ceased fishing.

The heavy fishery carried on during most of the summer and autumn in 1957 at the head of Passamaquoddy Bay reflected the concentration of herring there as indicated by the tagging. The movement towards Point Lepreau and Saint John County in July-August 1958 was confirmed by a substantial increase in the fishery in that area.

There is insufficient evidence from drift bottle experiments to establish any definite relationship between surface drift and herring movements. Tagged herring appeared at times to move neither with nor against the current. The surface layer may, however, be very shallow at such times and hence have no effect on the movements of fish. Generally, there was a greater tendency to swim against the current than in any other direction.

These tagging experiments have shown that herring moved freely in and out of Passamaquoddy and Cobscook Bays during the fishing season from May to October with some tendency to concentrate at the head of Passamaquoddy Bay. It is expected that the installation and operation of the proposed Passamaquoddy power dams would not affect the movement of herring to the Passamaquoddy area nor should it affect the distribution of fish except in Passamaquoddy and Cobscook Bays and immediately outside the dams. Herring should arrive outside the dams and filling gates in both Western and Letite Passages as before, but with filling gates open for only 5 to 6 hours each day (Trites, MS, 1959), the movement of fish into Passamaquoddy Bay will be delayed. This would affect the rate at which herring accumulate inside the bay. However, percentage recapture of tagged fish and the results of sonic sounder cruises in the Passamaquoddy area (Tibbo and Brawn, 1960) suggest that fishing mortality is low and there should be no reduction in the overall abundance of herring inside the bay. If the project is constructed, herring will not be able to enter Cobscook Bay directly from the outside. Entry into Cobscook Bay and exit from Passamaquoddy Bay will then be possible only through the turbines which lead into Cobscook Bay. As a result, movement into Cobscook Bay and away from both bays would be altered both in time and direction.

ACKNOWLEDGMENTS

The authors are pleased to acknowledge the co-operation of herring fishermen, plant operators and employees in returning tags. Grateful appreciation is extended to K. E. Bates, J. P. Cowie, F. W. Durant, and W. C. Hodges for the purchase and careful recording of tags. Records of returns in the United States were handled by H. C. Boyar, C. Larsen, and J. P. Wentworth.

Special acknowledgment is made of the co-operation of Mr L. W. Scattergood, U.S. Bureau of Commercial Fisheries, Boothbay Harbor laboratory, for permission to use the results of 10 tagging experiments carried out under his direction and for providing technical assistance in many of the other taggings.

The authors appreciate the extra time and effort given and the enthusiasm with which the technical personnel of the Pelagic Fish Investigation of the Fisheries Research Board of Canada at St. Andrews, N.B., carried out the field program.

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Oceanographic Activities of the Polar Continental Shelf Project¹

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ONE OF THE primary research objectives of the Canada Department of Mines and Technical Surveys' Polar Continental Shelf Project has been a detailed investigation of the characteristics and movement of the waters overlying the polar continental shelf and passing through the channels of the Canadian Arctic Archipelago. The program included sub-surface observations of temperature, salinity, and dissolved oxygen. Bottom samples and plankton collections were made at all stations, and at selected locations micro-thermal measurements were taken within the shallow, seasonal layer which forms directly under the ice.

Since the Project was initiated in 1958, two field seasons have been completed at Isachsen, N.W.T., with encouraging results. During the summer of 1959 emphasis was placed on the development of equipment and techniques by which precise oceanographic observations could be taken on the ice using a light, single-engined aircraft as the means of transportation.

Climatic conditions in the Isachsen area offer rather severe restrictions to normal flying procedures. The time during which fixed-wing aircraft may operate on the sea ice with the greatest efficiency is restricted to April and May. During this period the average air temperature is -15°F ; however, in 1959 oceanographic observations were undertaken at temperatures as low as -46°F . Under these conditions recording of sub-surface temperatures and the collection of water samples for salinity and dissolved oxygen determination require very careful handling and precise operating techniques.

PROCEDURES AND EQUIPMENT

To ensure uniformity in the operation of the deep-sea thermometers and to prevent the samples from freezing, the 1960 observations were carried out in a heated tent placed over the hole in the ice through which the instruments were lowered. Using four double-burner camp stoves it was possible to keep the temperature in the tent above freezing during the time the recordings were being taken. Water samples for salinity and dissolved oxygen analysis were stored in a warmed, insulated box and were sent back to the main base at Isachsen with the first available aircraft. These precautions proved successful in that only six water samples were lost through freezing during the 1960 field season.

Throughout the survey area the thickness of the sea ice varies from a maximum of over 8 m to a minimum of only a few centimetres. The average ice thickness measured in the frozen leads at each of the oceanographic stations was 190 cm. Areas where aircraft landings are possible are restricted to leads which

¹Received for publication January 13, 1961.

have frozen during calm conditions, thus producing a smooth, hard surface which is ideal as a landing strip for light aircraft. Fortunately, frozen leads of this type were common in the sea ice in the vicinity of Isachsen and little difficulty was experienced in landing close to the position determined for the oceanographic stations. In a few instances where ice conditions made it impossible to land a fixed-wing aircraft, the oceanographic camp was transported to the position by an S-55 helicopter. The time required at each site varied from 4 to 10 hours; however, at most stations the camp remained on the site for several days while the aircraft were busy with other commitments, or when weather conditions made flying impossible. The exact location of each station was determined by reference to a fixed beacon in the survey traverse or from Decca co-ordinates.

The oceanographic equipment which had been prepared for the Project consisted primarily of unmodified sea-going apparatus. Knudsen reversing water bottles fitted with double thermometer racks, and glass Copenhagen-type salinity sample bottles were used at all stations.

The ice drill which produced the best results was powered by a McCulloch Model 99 chain-saw engine fitted with a drilling turntable. In place of the normal earth auger attachment for this drill, a 12-foot adjustable section of diamond drill "A" rod fitted with a plate-type ice auger 10 inches in diameter was substituted. This equipment produced a clean, 10-inch-diameter hole through 6 feet of ice in approximately 15 minutes.

The winch used in 1959 was a small aircraft-target towing unit powered by a 1½-hp McCulloch engine, and proved quite satisfactory. However, in 1960 larger capacity winches were designed specifically to meet the weight and capacity specifications which were required. The 1960 oceanographic winch was built almost entirely of aluminum and was powered by a 2½-hp, 4-cycle Briggs and Stratton engine connected through a two-speed chain drive to a drum of 1500 m capacity. With minor modifications the machine proved quite satisfactory and reliable under all weather conditions that were encountered.

Four oceanographic stations were occupied in the Prince Gustaf Adolf Sea in May 1959. At the same time tests were carried out with Ott and Ekman current meters in an effort to determine if this type of meter was suitable for use in the area.

Between April 19 and June 3, 1960, a programme of 17 oceanographic stations was completed across the passages between Axel Heiberg Island and Prince Patrick Island and in a traverse extending 228 km to the northwest across the continental shelf (Fig. 1). In conjunction with the oceanographic observations taken at each site, supplementary records of soundings, ice conditions and local weather were kept at each location.

Oceanographic procedures at all stations included observation of sub-surface temperatures, collection of samples for salinity and dissolved oxygen determination and plankton analyses, making vertical net hauls for zooplankton collections, and taking cores of the bottom sediments. Bathythermograph observations were made at all stations, and at one location a series of wire-angle observations was taken using a Japanese-type wire-angle gauge.



FIG. 1. Location of Polar Continental Shelf Project (1960) oceanographic stations.

RESULTS

Knowledge of the bathymetry of the continental shelf in the vicinity of Isachsen was virtually non-existent prior to the 1959 survey. The few scattered soundings that were available gave indication of relatively deep channels to the north and south of Ellef Ringnes Island, but little evidence of the extent of the continental shelf. The IGY soundings along the track of Ice Island T-3 defined the position of the seaward margin of the continental shelf at several locations along the western arctic coast (Crary and Goldstein, 1957; Collin, 1959). Information from the U.S.S.R. indicated a steeply dipping continental slope and indentations in the continental shelf along the off-shore extensions of Sverdrup Channel and the Prince Gustaf Adolf Sea. Soundings taken within the last two years give a much clearer picture of the bathymetry in this region.

In the Cape Isachsen area the continental shelf extends out from shore a distance of 170 km, with water depths of about 500 m at the seaward edge.

Present soundings indicate that the shelf profile at Cape Isachsen is composed of three zones. The inshore section extends to a distance of 9 km at a gentle slope of less than $\frac{1}{2}^\circ$. Beyond this point the coastal slope merges with an extensive, plateau-like area with an almost uniform depth of 500 m. This platform ends abruptly at the edge of the continental slope, at which position the depth increases from 500 m to over 2000 m at a slope of slightly greater than $1\frac{1}{2}^\circ$. The greatest depth recorded on the continental slope during the 1960 field season was 1239 m.

Within the passages to the north and south of Ellef Ringnes Island, channels having a depth of 400 to 500 m were found parallel to the main axis, predominantly along the northern sides of the straits. It does not appear that the deep trough in Peary Channel extends through the continental shelf into the Arctic Basin, although in the Prince Gustaf Adolf Sea there is evidence that the less well-defined channel along the Ellef Ringnes coast is continuous through the continental shelf.

Temperature and salinity graphs (Fig. 2) have been produced from the five

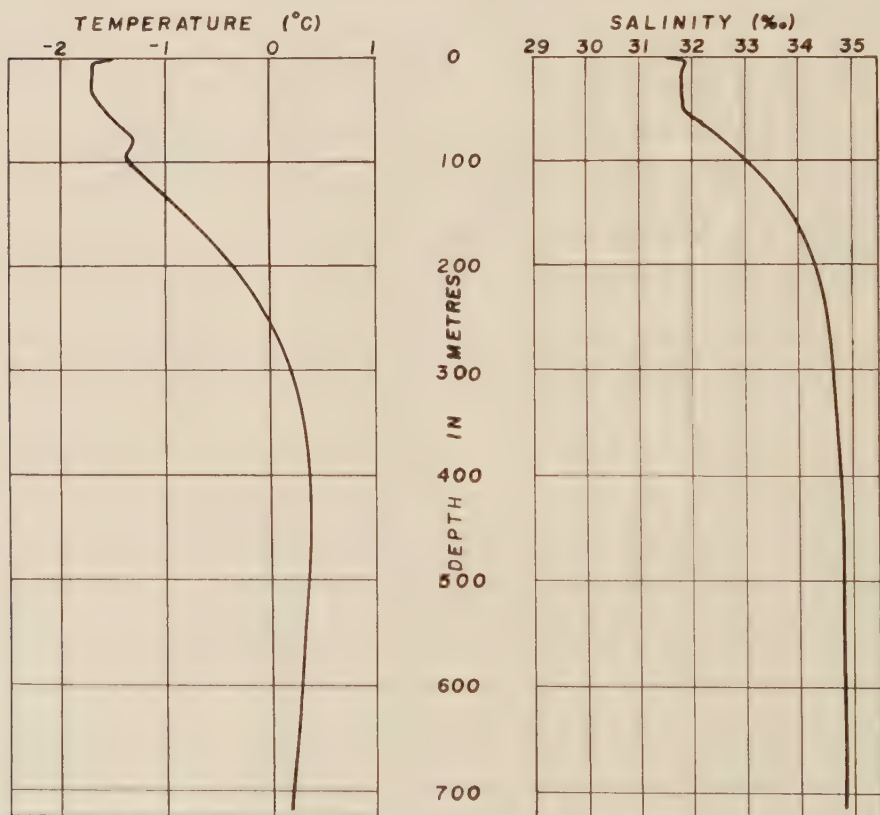


FIG. 2. Average temperature and salinity, Arctic Ocean stations, May 1960.

oceanographic stations (Table I) which were occupied across the continental shelf in the vicinity of Ellef Ringnes Island.

TABLE I. Positions of Polar Continental Shelf Project (1960)
Arctic Ocean Stations.

Date	PCSP Station	Latitude N	Longitude W	Depth <i>m</i>
April 2	2	79° 25'	105° 56'	143
May 30	14	80° 42'	112° 50'	1239
May 30	15	80° 12'	109° 45'	499
May 30	16	79° 37'	106° 54'	340
May 31	17	79° 52'	108° 20'	487

The data obtained at these stations show that the characteristics of the water on the continental shelf are generally similar to those encountered in the Arctic Basin.

The temperature curve shows a surface layer having temperatures of less than -1.6°C to a depth of 50 m, a definite negative thermal gradient at 75 to 100 m and temperatures greater than 0.0°C between 250 and 800 m.

The interesting temperature structure at 75 m is mentioned by Worthington (1953a, b) and is shown to be a typical feature of the Beaufort Sea. However, at the 1957 and 1958 Ice Island T-3 stations between latitudes 78°N and 83°N there is little indication of this phenomenon (Farlow, 1958; Collin, 1959). Worthington (1953a) suggests that this gradient appears to be the last remnant of a seasonal thermocline which must have been formed in the ice-free areas of the Beaufort Sea during the summers of 1950 and 1951.

A similar explanation may be called upon to account for the appearance of this type of thermocline at the continental shelf stations. At the 1957 and 1958 T-3 stations the ice island was invariably surrounded with sea ice of 10/10 concentration. In comparison, the region of the Polar Continental Shelf Project Stations 2, 15, 16 and 17 is well known as an area of pronounced ice movement. Wide leads form in this region during late May and persist throughout the summer. Thorsteinsson reported several miles of open water in the area off Cape Thomas Hubbard, Axel Heiberg Island, in June 1957 (Blackadar, 1958) and in the summers of 1959 and 1960 leads up to 2 miles wide were reported in the vicinity of Ellef Ringnes Island. Much larger areas of open water were observed to the north and west of Meighen Island in September 1960. It is estimated that at the time of maximum extent 6% of the sea surface within 40 miles of the north-west coast is exposed as open water. The significance of this relatively small area of ice-free water would appear to be negligible. However, the 1960 oceanographic observations seem to indicate that throughout the year, open water areas have a marked effect on water characteristics within the upper 100 m and there is a considerably larger percentage of open water forms in this region than has been hitherto observed.

On the continental shelf the Atlantic layer, as limited by the zero isotherms, was found to extend from approximately 250 m to the bottom at 500 m. At Station 14, on the continental slope, the Atlantic layer was located between 250 and 850 m. The thickness of this layer and the depth of maximum temperature, 0.43°C at 500 m, correspond remarkably well with the information presented by Timofeev (1957).

The general slope of the isobaric surfaces, downward toward the coast, indicates a weak, southwesterly water movement.

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Correlation of Morphological and Intra-ocular Measurements in the Atlantic Salmon (*Salmo salar*) Yearling^{1, 2}

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ABSTRACT

In the Atlantic salmon yearling, correlation among various morphological measurements is of a higher order than correlation of various intra-ocular measurements. While the latter correlation is positive, it is not of a high enough order to serve as a useful predictive device. Correlation between intra-ocular measurements from the left and the right eyes is also of a low order.

INTRODUCTION

IN AN EARLIER histophysiological investigation (Brett and Ali, 1958) of the Pacific salmon (genus *Oncorhynchus*) retina, the thicknesses of the retinal epithelial pigment and cone layers were expressed as percentages of the retinal thickness in the construction of graphs describing the rates of light and dark-adaptation of the retinal elements. In a later, more comprehensive investigation (Ali, 1959) more than 9,000 eyes were examined belonging to various stages of 4 species of Pacific salmon (sockeye, *O. nerka*; coho, *O. kisutch*; pink, *O. gorbuscha*; chum, *O. keta*). It was then concluded that, although the retina and consequently the various retinal elements composing it are thicker in an older, larger stage (e.g. smolt) than in a younger, smaller stage (e.g. alevin), the thicknesses of the retinal elements in the retinae of fishes of the same age group did not vary in direct proportion to the thicknesses of the retinae but did so at random. In view of this, in the graphs constructed to show the effect of various light conditions on the retinal pigment and cone layers, the thicknesses of these layers were plotted directly. These graphs proved quite satisfactory and served their purpose well. In subsequent investigations (Ali and Hoar, 1959; Ali, 1960a), with the Pacific salmon retinae also the same method was followed. In all these studies, graphs were also constructed wherein the thicknesses of the retinal pigment and cone layers were expressed as percentages of the retinal thickness; and indeed, in a recent study (Ali, 1960b) of the retina of Florida chamelon (*Anolis carolinensis*), graphs constructed using direct thicknesses as well as percentages have been presented for comparison. However, since the latter did not differ significantly from those constructed using direct thicknesses and since the exact relationship between the thickness of the retinal elements and the thickness of the retina was not known, the percentages were not accepted as consistent proportions.

In view of this background and in view of the fact that an extensive survey of the histophysiology of the Atlantic salmon retina has been undertaken, it appears desirable that an investigation wherein the relationships among morphological and intra-ocular measurements are ascertained might prove helpful in the

¹Received for publication August 25, 1960.

²This investigation was supported by an operating grant from the National Research Council (Canada) to M. A. Ali.

interpretation of retinal responses to various experimentally induced light conditions.

Moreover, although the length-weight relationship in the Atlantic salmon is known (Hoar, 1939; Carlander, 1953) no investigation has been undertaken to establish the relationship among other morphological and histological characteristics. It is felt that this study will contribute, at least to a small extent, in this regard also.

MATERIAL AND METHODS

MATERIAL

Yearlings obtained from Margaree Hatchery, Frizzleton, Nova Scotia, in March 1960 and reared in the Fish Research Laboratory of the Memorial University, were used. They were kept in wooden tanks with constantly aerated and refrigerated running water. While in the laboratory they were exposed to 16 hours light (25 ft-c) per day. Temperature of the water ranged from 4°C to 10°C. They were fed ground beef liver twice daily.

METHODS

SAMPLING. Fifty fish were sampled under identical conditions (25 ft-c; 8°C) on May 10, 1960, between 10.30 and 11.00 a.m. These were fixed in standard Bouin's fixative. After death, their eyes were punctured at the sclero-corneal junction in order to allow better fixation of the retina. After 48 hours in the fixative, the fish were transferred to 70% alcohol and their lengths, weights and head diameters measured. The eyes were then enucleated and separated. The diameter of each eye was measured at five planes and the average determined. After this, the cornea and lens were removed.

HISTOLOGICAL. The eyes were dehydrated in ascending strengths of alcohol, cleared in xylene and inbedded in paraffin (Fisher Tissuemat; M.P. 54-56°C). Sections were cut at 8 microns, stained with Harris' haematoxylin and counterstained with eosin (water soluble; 5%). The prepared sections, which were mounted in Canada balsam were dried at 37°C before being examined.

MEASUREMENTS. In all eyes, the thicknesses of the retinae, retinal epithelial pigment and cone layers were measured at 5 locations (3 in the peripheral regions and 2 in the region of the fundus). In each case the average of the 5 measurements was considered as the true thickness. The method followed in measuring the various layers was the same as the one used in a previous investigation (Ali, 1959).

STATISTICAL. The correlation carried out was of the simple two-variable rectilinear type. Examination of scatter diagrams indicated that where a significant degree of correlation was in evidence, a straight line fit was not inappropriate. Data for the 50 fish were left ungrouped and the linear correlation coefficients were calculated (Croxtan and Cowden, 1955). Confidence limits of correlation coefficients were calculated using the z-transformation of Fisher (1950).

RESULTS

A coefficient of correlation was calculated for each combination of two of the following variables.

Morphological measurements	
Cube root of the weight.....	$\sqrt[3]{W}$
Length (to fork of tail).....	L
Head diameter.....	H
Left eye thickness.....	E
Intra-ocular measurements (left eye)	
Retinal thickness.....	R
Cone layer thickness.....	C
Pigment thickness.....	P

The cube root of the weight was used, rather than the weight itself, in order to reduce the weight variable to a dimension approximately comparable with that of the other variables, which were all linear.

The coefficients of correlation found are shown in Table I. If the value

TABLE I. Coefficients of correlation between various sets of morphological and intra-ocular measurements. See text for explanation of symbols. Graphs (Fig. 2-7) are presented for sets of measurements marked by an asterisk (*).

L	+0.92					
H	+0.88	+0.84				
E	+0.88	+0.87	+0.82			
R	+0.31	+0.20	+0.26*	+0.22		
C	+0.43	+0.27*	+0.19	+0.29	+0.43*	
P	+0.34	+0.30	+0.41*	+0.31	+0.42*	+0.44*
$\sqrt[3]{W}$	L	H	E	R	C	

0.70 is taken as the criterion of a useful degree of correlation for predictive purposes, the coefficients found divide quite clearly into those which show useful correlation and those which do not.

COMPARISONS OF MORPHOLOGICAL CHARACTERS

All four of the external morphological characters measured were highly correlated (top 3 rows in Table I). The correlation of the lengths of the fish with the cube root of their weight yielded the highest coefficient, +0.92. As an alternative indication of this relationship, the coefficient of condition of each fish was calculated using the formula $(100 W) \div L^3$, with the weights recorded in grams and lengths in centimetres (Hoar, 1939). As shown in the accompanying histogram (Fig. 1), the coefficients of condition ranged from 0.4 to 1.0, all but 4

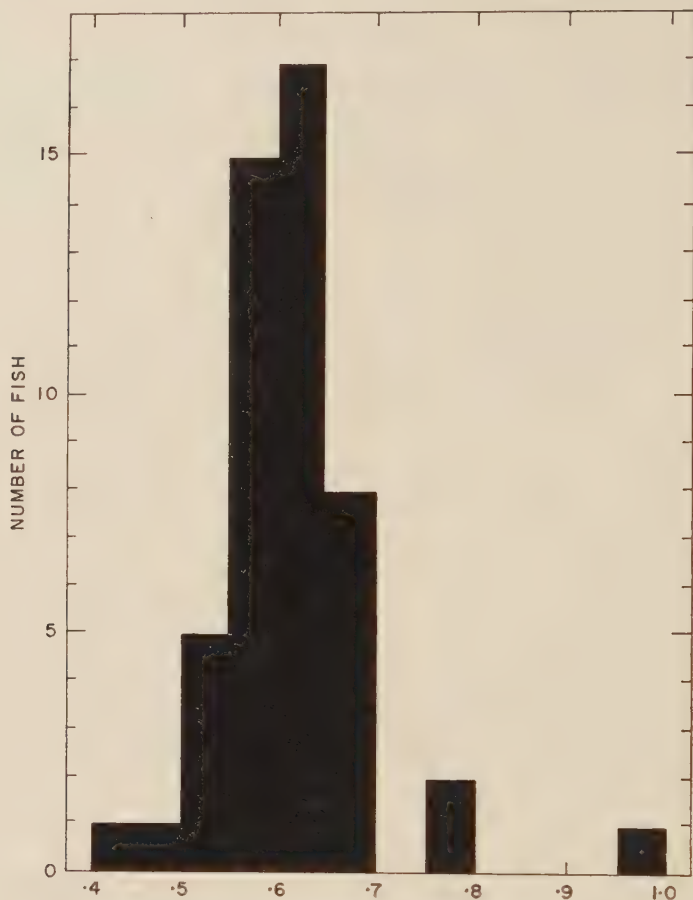


FIG. 1. Histogram showing the frequency distribution of coefficients of condition of the 50 fish used in this investigation.

cases falling in the 0.5 to 0.7 range. This gives an indication of the degree of dispersion in the length-weight relationship which is compatible with the high coefficient of correlation shown.

COMPARISONS OF INTRA-OCULAR CHARACTERS (Fig. 2-4)

Correlations between thickness of retina, cone layer and pigment all yield positive coefficients, but of such low magnitude (0.42-0.44) that they would not be useful for prediction (the 2 right-hand columns of Table I). The highest coefficient in this group, +0.44, has 95% confidence limits of +0.64 and +0.19. At this level of significance, therefore, no coefficient in this group could reach the +0.70 limit of "usefulness". This low level of correlation among the intra-ocular measurements is surprising; it indicates that the characters measured vary independently, for the most part.

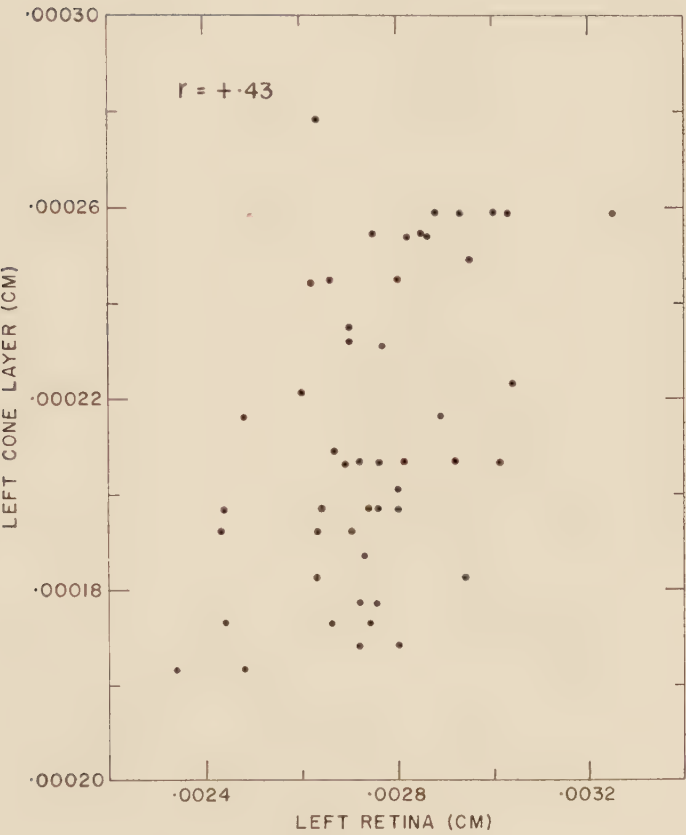
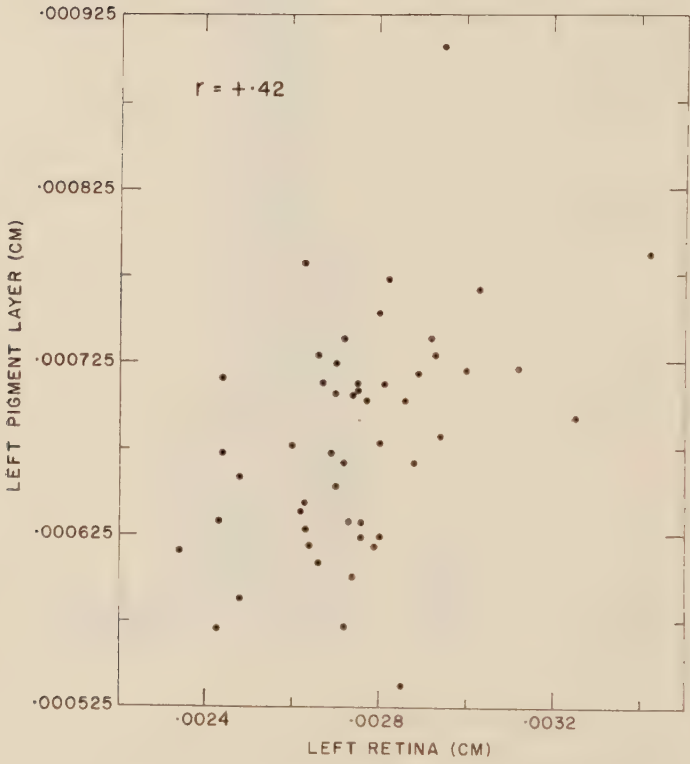


FIG. 2. Thickness of cone layer plotted against thickness of retina, for the left eye.



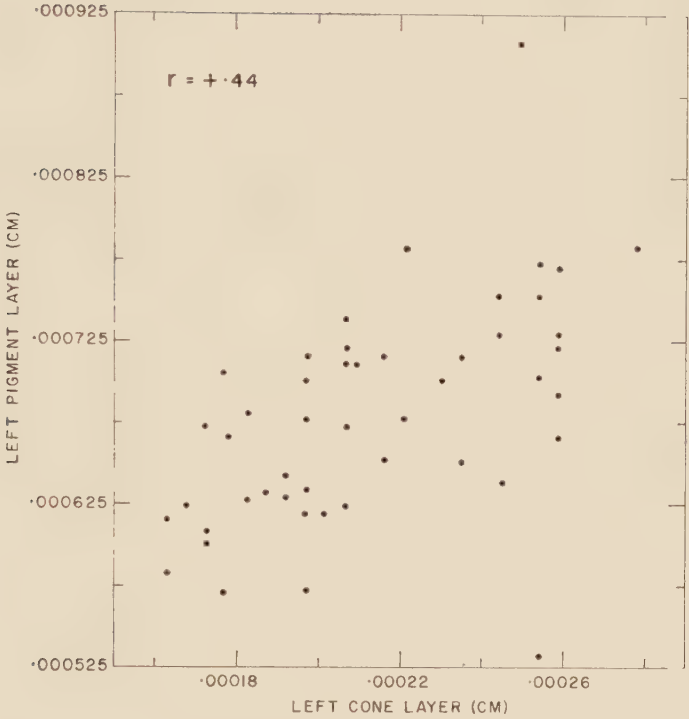


FIG. 4. Thickness of pigment layer plotted against thickness of cone layer, for the left eye.

COMPARISONS OF INTRA-OCULAR WITH EXTERNAL CHARACTERS (Fig. 5-7)

If the correlations among intra-ocular measurements are not large, then the correlations between intra-ocular and the highly-correlated external morphological measurements cannot be expected to be large either, which is in fact the situation (Table I). The coefficients of correlation between intra-ocular and morphological measurements are in fact somewhat smaller than those among the intra-ocular measurements, as seems natural.

COMPARISON OF THE TWO EYES OF EACH FISH (Fig. 8-11)

As a further step, the eye diameter and each of the intra-ocular measurements of the left eye of each fish was compared with the corresponding measurement from the right eye. The resulting correlation coefficients follows:

Measurement	Eye diameter	Retina	Cone layer	Pigment layer
Coefficient	+0.82	-0.03	+0.39	+0.29

Only the external measurement, eye diameter, shows a large correlation between left and right eyes. Therefore, while for each fish the size of the two eyes tends to be about equal, this is not so, or at most weakly so, for the thickness of the retinal, cone and pigment layers in the two eyes.

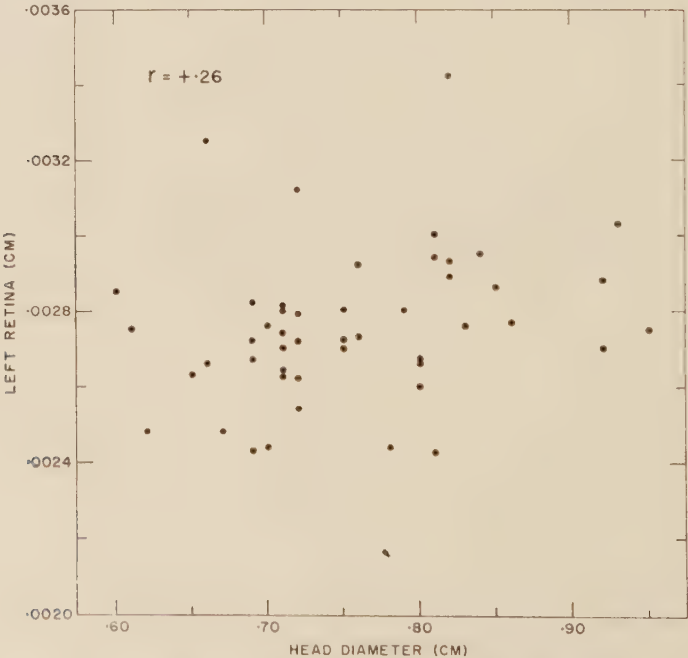


FIG. 5. Thickness of left retina plotted against head diameter.

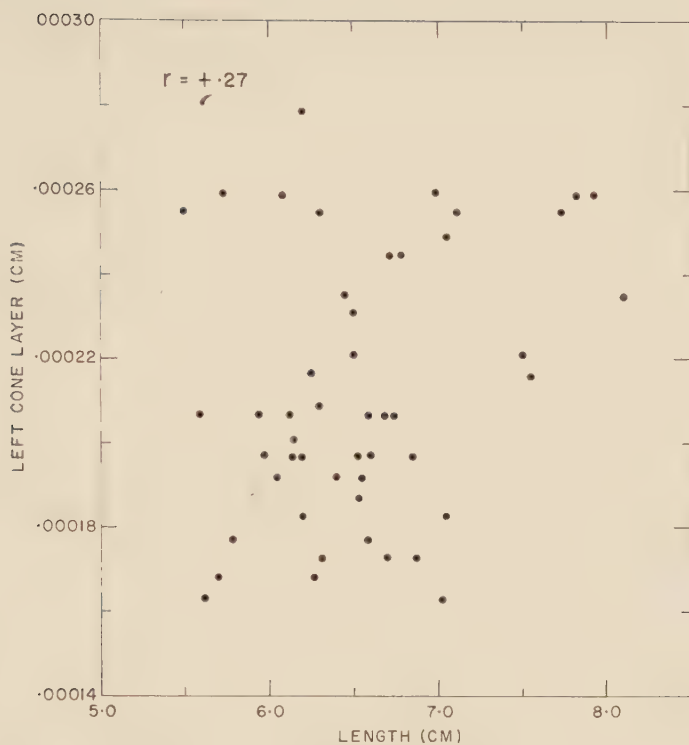


FIG. 6. Thickness of cone layer of the left eye plotted against body length.

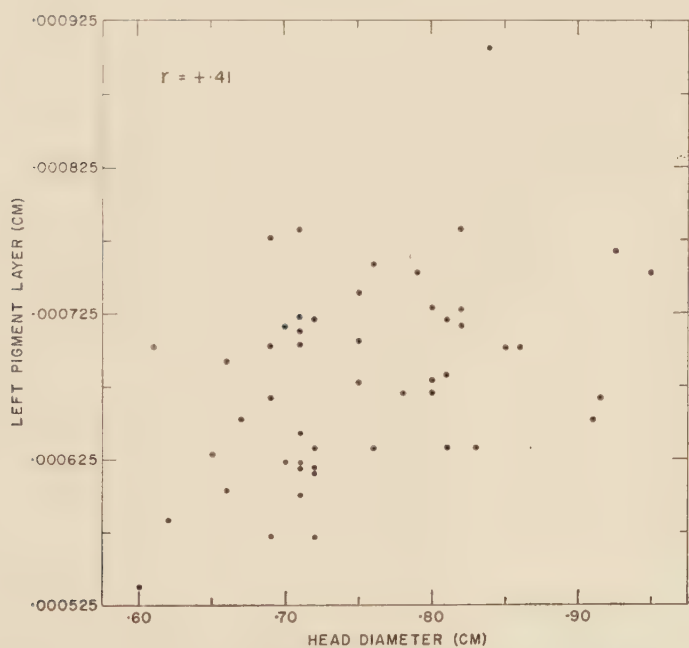


FIG. 7. Thickness of pigment layer of the left eye plotted against head diameter.

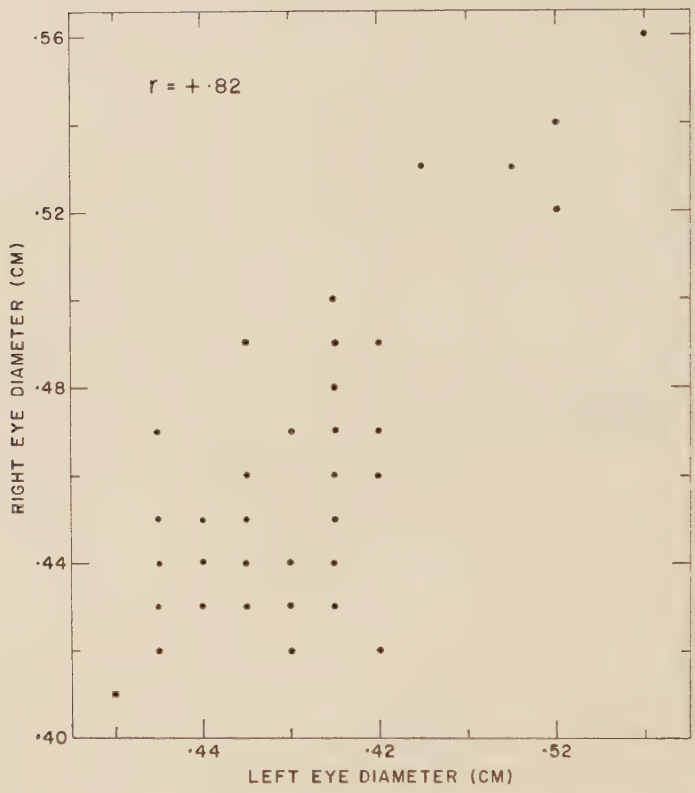


FIG. 8. Right eye diameter plotted against left eye diameter.

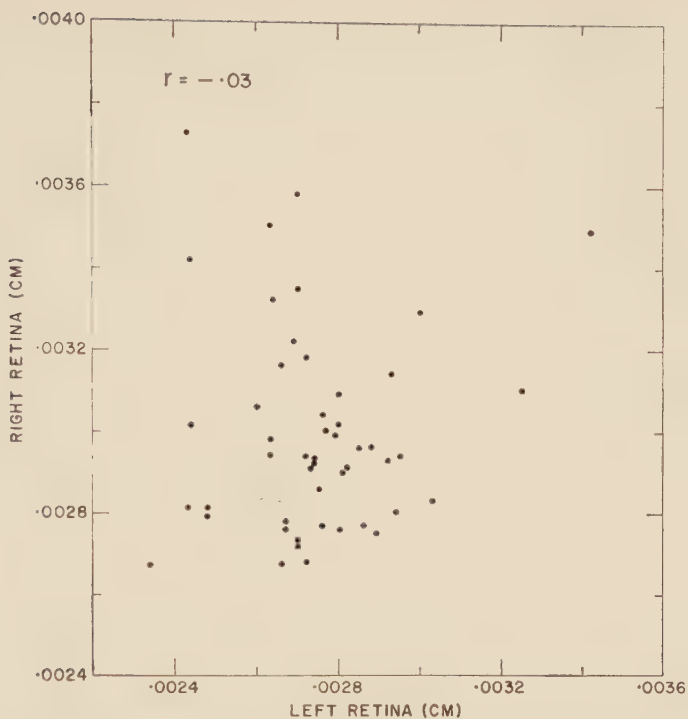


FIG. 9. Thickness of retina of the right eye plotted against thickness of retina of the left eye.

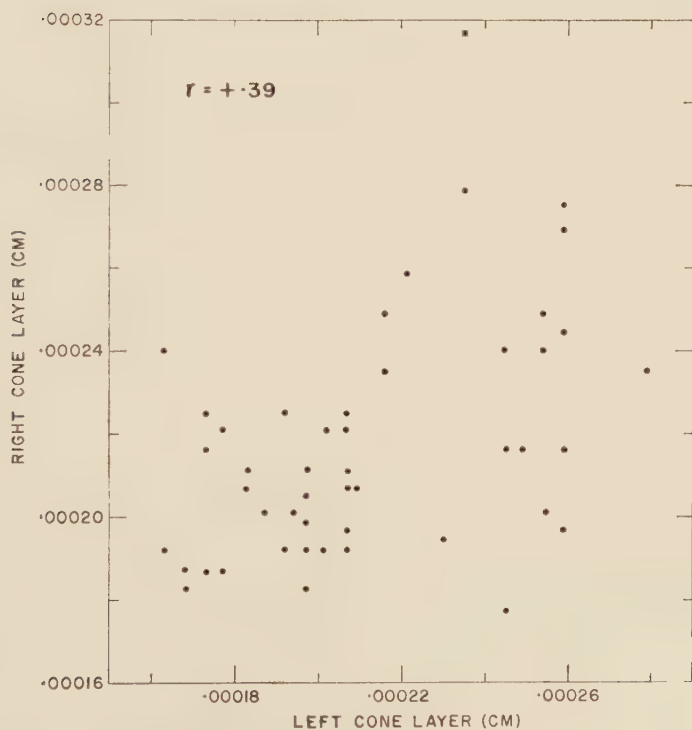


FIG. 10. Thickness of cone layer from the right eye plotted against thickness of cone layer from the left eye.

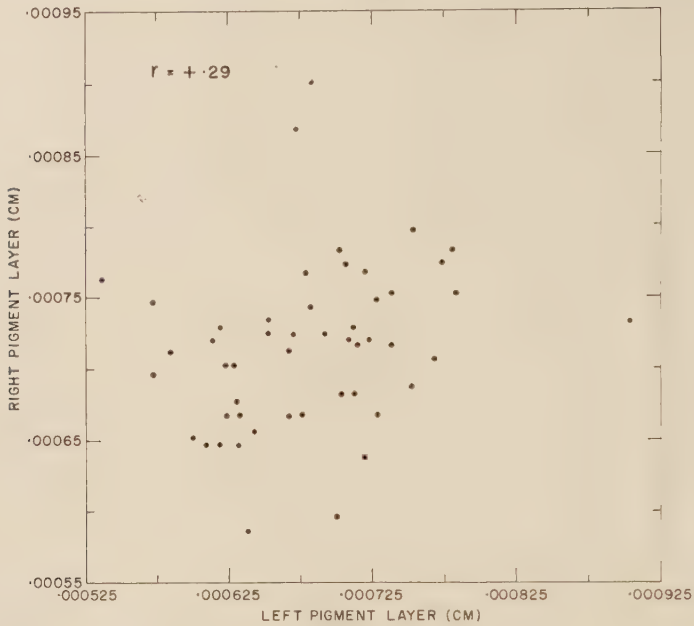


FIG. 11. Thickness of pigment layer of the right eye plotted against thickness of pigment layer from the left eye.

DISCUSSION

There is a possibility that the results above may have been influenced, to a minor extent, by the histological technique. It is conceivable that not all eye sections were cut on exactly the same plane. The eye is circular, and during embedding in the paraffin one may have been oriented in one way and another somewhat differently. Besides, although every attempt was made to make the microscopic measurements from the sections of the eye taken from the centre (viz. the exact middle dividing line), it is possible that not all sections measured were from exactly the same region. This makes for a margin of inaccuracy in the intra-ocular measurements, which undoubtedly exceeds that of the morphological measurements. However, the possible variability from this source seems small, quite inadequate to account for the marked absence of useful correlation among the intra-ocular measurements.

Since technical variability can be discounted, there remain two principal possibilities. 1. At the light intensity used the retina, cone layer and pigment layer may each be of more or less constant thickness within each eye, each congenitally determined and changing slowly if at all; the thickness of each of these layers being largely independent of the other layers within the same eye, independent of the thickness of the same layer in the eye of the other side of the fish, and independent of fish size. 2. Alternatively, we might imagine that

retina, cone layer and pigment layer vary continuously in thickness (within the numerical limits shown in our figures) over short time periods, of the order of hours or days; each eye and each layer varying independently of the other, independently of the (constant) general external illumination, and independently of the general physiological condition of the fish (changes in which reach the two eyes equally).

SUMMARY

1. Length, cube root of weight, head diameter, and eye diameter show large correlations ($+0.82$ or more) among themselves, in Atlantic salmon yearlings of 55–80 mm fork length.
2. Coefficients of conditions ($100W \div L^3$) range from 0.40 to 1.0 with all but four cases falling in the 0.50 to 0.70 range.
3. Intra-ocular measurements made by histological methods, viz. thicknesses of retina, cone layer and pigment layer, show poor coefficients of correlation (0.42–0.44) among themselves, and even smaller correlations with any of the external morphological measurements.
4. The results suggest that at a given moment the internal ocular structure is peculiar to each eye of each fish, and is practically independent of fish size over the range examined.

ACKNOWLEDGMENTS

Our thanks are due to Mr J. M. Butler and Mr A. J. Baxter of the Fish Culture Branch of the Canada Department of Fisheries for kindly supplying the fish used in this investigation. The assistance of Miss Judith Press and Mr D. Mercer with histology and statistical treatment of the data is gratefully acknowledged.

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A Note on the Morphology of the Basins of the Great Lakes¹

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ABSTRACT

Neumann (1959) has suggested the elliptic sinusoid as a model for an average lake. Area-depth curves for the Great Lakes are compared with the corresponding curves given by the Neumann model which, it is suggested, should be useful in idealized calculations on a lake.

THE PRESENCE of the Great Lakes as a closely connected series of large basins must first be thought as requiring unusual explanation. However the relief of the basins is only about 1 in 3000, and Hough (1958) has concluded that differential glacial scouring of preglacial drainage channels in relatively soft sedimentary rocks (added possibly, in the cases of Lake Michigan and Lake Huron, to ancient collapse of salt domes) provides a reasonable explanation of them. The 5 lakes in a series will then be considered as being due to the chance workings of glacial scour, and drainage, and to local peculiarities in eroded sedimentary forms rather than to more subtle results of basic precambrian structure.

The resulting peripheral shapes of each of the Great Lakes differ substantially, but the area depth profiles shown in Fig. 1 have much the same form, save for Lake Erie which is much more shallow than the others, and Lake Superior which has a very irregular basin. These profiles were obtained from published charts of the Canadian Hydrographic Service and, for Lake Michigan, of the United States Lake Survey. The published soundings are presumed complete and accurate for all Lakes except for a central area of Georgian Bay and this gap was partially filled by soundings taken during surveys by R/V *Porte Dauphine* in 1959. The shorelines were arbitrarily restricted by exclusion of certain bays and inlets, so that other assessments might differ from these by a few per cent.

¹Received for publication, November 7, 1960.

Mr K. Haessler did the planimetric work with a planimeter kindly made available by Mr J. Murray, Conservation Branch, Ontario Department of Planning and Development.

The profiles are useful in volumetric calculations such as the determination of total heat content from bathythermographic surveys.

An interesting comparison of the average depth ($\bar{D}$) and maximum depth (D_m) of over one hundred lakes by Neumann (1959) showed that the mean ratio

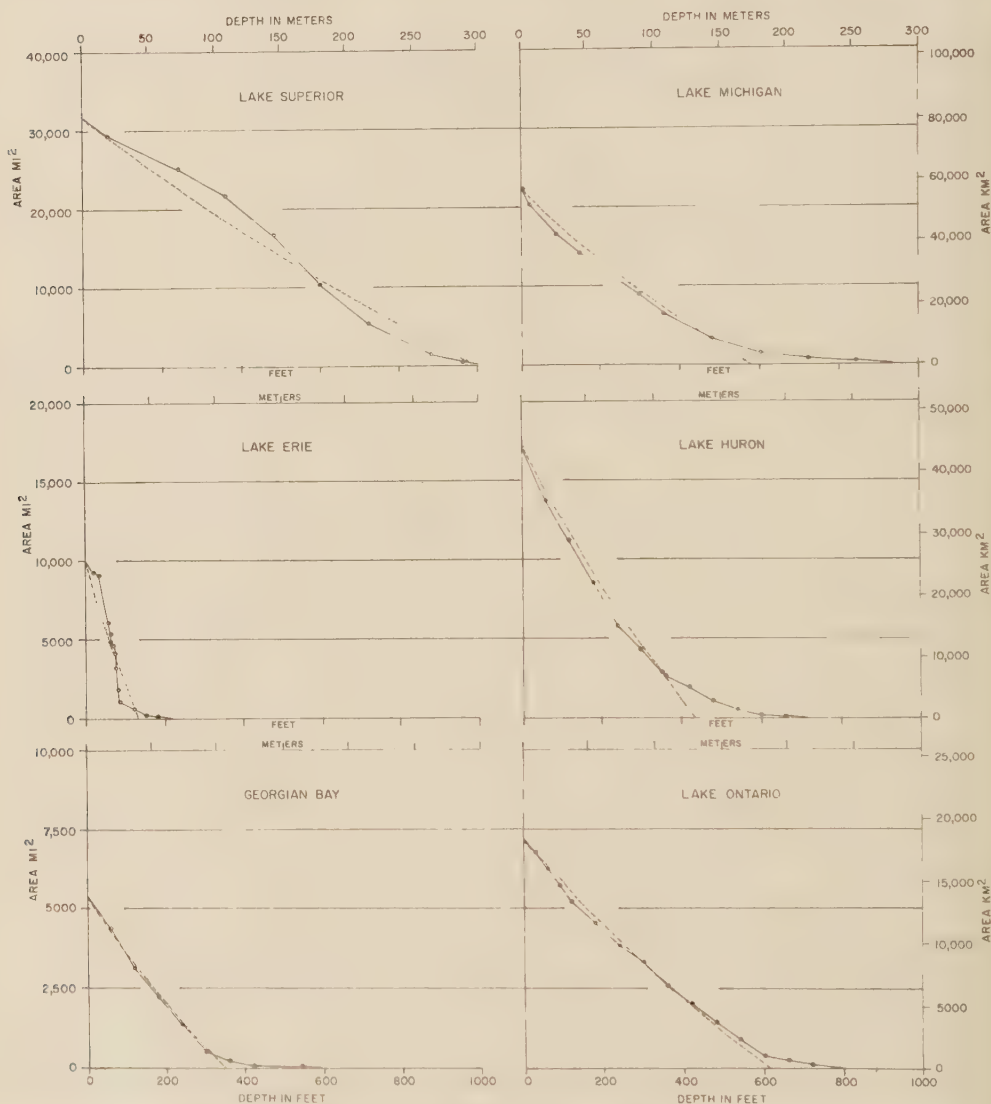


FIG. 1. Area versus depth: solid line, areas determined from hydrographic charts; dotted line, areas by Neumann's model.

of the two, as observed in nature, is 0.467. He proposed that the best model of an average lake basin is an elliptic sinusoid, for which $\bar{D}/D_m = 0.463$. Neumann plotted (his fig. 1) D_m versus $\bar{D}$, but it seems better to plot as well the ratio $\bar{D}/D_m$ versus $\bar{D}$ to show the scatter as in Fig. 2. Table I gives the averages of the ratio for various size classes of lakes and the average deviations.

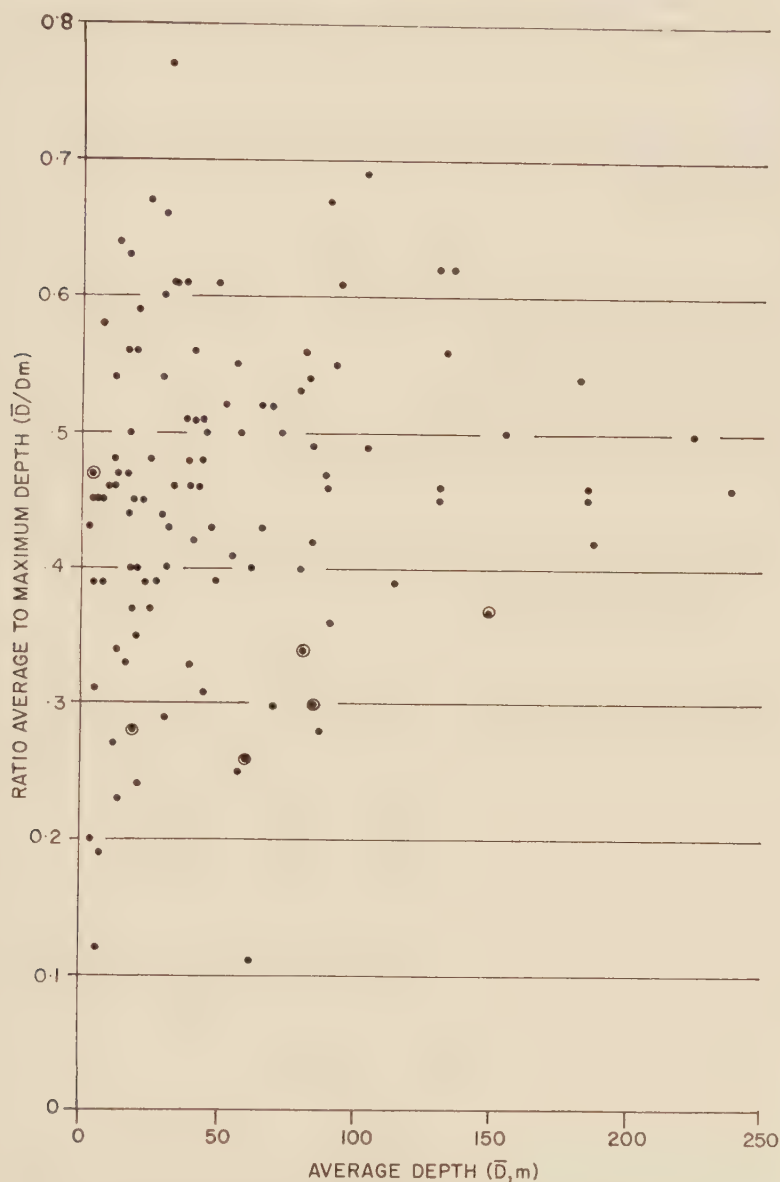


FIG. 2 Ratio of average depth and maximum depth versus average depth (values for the Great Lakes are accentuated); after Neumann (1959).

TABLE I

	Range of average depth, meters		
	0-50	50-100	100-200
Number in sample	71	26	14
Average $\bar{D}/D_m$	0.45	0.43	0.50
Average deviation	0.10	0.11	0.08

The choice of an elliptic sinusoid is not, therefore, critical but is a very convenient one, since the formulae associated with it are so simple (Neumann, p. 927). If the lake surface be approximated by an ellipse of semi-major and -minor axes, a and b , and the amplitude of the sinusoidal profiles is D_m , the volume V is:

$$V = 4\left(1 - \frac{2}{\pi}\right)ab D_m \quad \dots \quad (1)$$

and the surface area is $A = \pi ab$. This suggests that for purposes of comparison of maximum depth with other lakes, (1) be used to calculate an *effective* maximum depth $\bar{D}_m = 2.16 \bar{D}$, the citation of $\bar{D}_m$ having much more significance, morphologically speaking, than the single measurement D_m . In the case of lakes with complicated bottom shapes, D_m is a single value with only very limited significance.

Table II gives the pertinent characteristic values for the Great Lakes. Fitting values of a and b is somewhat arbitrary of course. As noted above, the figures cited differ from those quoted by the United States Lake Survey and Canadian Hydrographic Service.

TABLE II. Hydrographic data for the Great Lakes

	Area	b	a	Vol.	D_m	$\bar{D}$	$\bar{D}_m$
	mi^2	mi	mi	mi^3	ft	ft	ft
Superior	31,700	50	202	2,796	1,302	464	1,000
Michigan	22,400	45	158	1,134	923	268	579
Georgian Bay	5,380	30	57	164	...	161	348
Huron	17,350	50	110	664	750	202	436
Erie	9,970	30	106	116	210	61	132
Ontario	7,250	25	92	390	778	284	615

It can be shown that the area of the level surface at depth z of the model lake corresponding to the actual lake is:

$$A_z = \frac{4ab}{\pi} \left(\cos^{-1} \frac{z}{D_m} \right)^2 \quad \dots \quad (2)$$

and the dotted curves in Fig. 1 give the figures calculated from (2) for each lake. The assumed elliptic sinusoid model is shown to be good for Michigan, Huron, Ontario and Georgian Bay but poor for Superior and Erie.

It appears that Neumann's model could be useful, especially because of its arithmetic simplicity, in idealized calculations in which preservation of volumetric change with depth is important.

ACKNOWLEDGMENT

This work was made possible by a grant and facilities provided by the Ontario Department of Lands and Forests.

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NOTES

Occurrence of Two Species of Juvenile Rockfish in Queen Charlotte Sound

On August 25, 1960, scientists aboard the *John N. Cobb* sighted and recovered a Japanese glass fishing float, $7\frac{1}{2}$ miles NNW of Triangle Island in Queen Charlotte Sound (Lat. $50^{\circ} 59.4' N$, Long. $129^{\circ} 2.8' W$). The 12-inch (30-cm) diameter float was covered with $\frac{1}{4}$ -inch (6-mm) cotton cord webbing. Attached to the webbing was a large mass (Fig. 1) of gooseneck barnacles (*Lepas anatifera*).



FIG. 1. Barnacle mass attached to the Japanese glass fishing float.

Upon close observation of the barnacle mass 8 juvenile rockfish, all under 55 mm in length, were discovered. The young rockfish had apparently adopted the mass of barnacles for cover or feeding.

Information on the distribution and habitat of juvenile rockfish (*Sebastes*) off the North American coast is rather fragmentary. Partlo (1950) reports that young rockfish, tentatively identified as *Sebastes pinniger*, constitute one of the main food items of albacore taken off British Columbia, and Powell *et al.* (1952) report that juvenile *Sebastes alutus* and *S. crameri* constitute major food items for albacore taken off the Washington and Oregon coasts.

The 8 rockfish found among the barnacles could be divided into two groups by their general appearance. Four of the rockfish had distinct black bands over a yellowish-gold background. The others were of a brownish-red colour with no distinct markings (Fig. 2). Meristic and morphometric data for the specimens are given in Table I, and were compared with those given by Phillips (1957). Specimens having black stripes were identified as *Sebastes nigrocinctus* and those having a brownish-red colour appeared to be *Sebastes caurinus*.

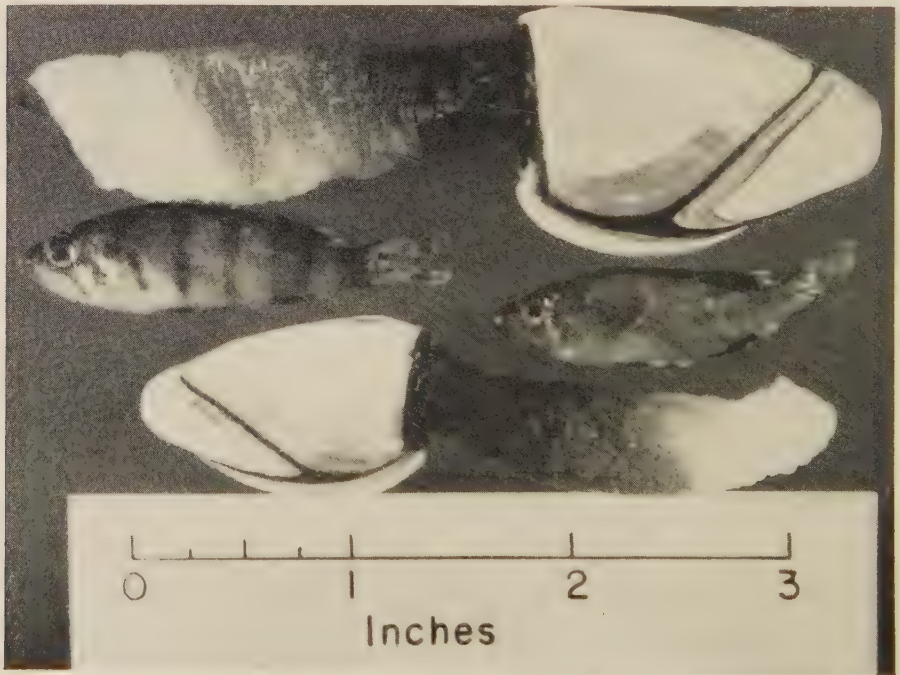


FIG. 2. Two species of juvenile rockfish with representative specimens of the gooseneck barnacle. Left—*Sebastes nigrocinctus*; right—*S. crameri*.

TABLE I. Meristic and morphometric data of 8 rockfish specimens taken from the barnacle mass.

	Individuals with black bands				Individuals without black bands			
	1	2	3	4	1	2	3	4
Total length, mm	47	47	45	40	52	45	42	43
Standard length, mm	40	39	38	33	42.5	38	36	36
Head length, mm	15	15	14	13	17	14.5	13.5	12.5
Head length into st. length	2.66	2.60	2.71	2.54	2.5	2.62	2.67	2.88
Gill raker count	30,29	26,-	28,28	27,26	30,29	28,29	27,28	28,28
Lateral line pores	49,48	49,46	47,45	49,47	41,38	43,44	44,40	40,41
Head Spines <i>Absent</i>	Supraocular—on 2 individuals the nuchial also could not be distin- guished.				Supraocular, coronal, nuchial.			

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Received for publication December 8, 1960.

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Abnormalities in Lake Erie Whitefish

During an investigation of the Lake Erie commercial whitefish (*Coregonus clupeaformis*) catch in the years 1947 to 1949, notes were made on the morphological appearance of each fish handled. Visible abnormalities were noted in 11% of 1709 whitefish examined. Most of the fish examined belonged to the 1944 year-class. In 1956, Dr R. G. Ferguson, Division of Research, Ontario Department of Lands and Forests, at the writer's request, examined a sample of 108 Lake Erie whitefish and found 10% had abnormal caudal fins. By contrast, no visible skeletal abnormalities were recorded from over 10,000 whitefish examined between 1950 and 1960 from Heming Lake, Manitoba, situated at Lat. 54° 30' N.

The most common abnormality, found in 9% of the sample, was that the dorsal lobe of the caudal fin was considerably shorter than the ventral lobe. Intergrades between abnormal and normal fins may have existed, but only obvious differences were recorded. Apparently the upper portion of the hypural plate was considerably thickened, tending to shorten the rays of the dorsal lobes of the fin.

The caudal fin appeared lunate rather than forked in 1% of the sample. Extreme humpbackedness was noted in 0.5% of the sample.

The most striking but least frequent deformities (less than 0.5%) are shown at the top and bottom of Fig. 1. The vertebral columns of these fish are reduced in length by the fusion of adjacent centra. In both fish at least 17 vertebrae are compacted. The neural and haemal processes appear to be present in normal numbers. The whitefish shown in the middle of the photograph exhibits two compacted vertebrae in the mid-region. Such minor anomalies are not recognizable from external inspection and would escape detection, so it is quite probable that more than 11% of the sample had skeletal abnormalities of some type.

Skeletal anomalies are not rare among freshwater fishes, as Scott (1951) found that 5.4% of Lake Erie ciscoes (*Leucichthys artedii*) had vertebral deformities, and Gosline (1947) considered 5.8% of 1058 *Poecilichthys exilis* to be deformed. Extremely asymmetrical tails (similar to those described above) were noted by Stone (1938) among the ciscoes (*L. artedii*) of the deep-bodied type in Irondequoit Bay, Lake Ontario.

McHugh and Barraclough (1951) described an abnormality in carp and pointed out that fusions and deformities involving limited numbers of vertebrae are not uncommon in natural populations and most commonly occur at the posterior end of the vertebral column. O'Donnell (1945) described an abnormal carp in which the last 8 precaudal and 17 caudal vertebrae were completely fused and concluded that the condition resembled *arthritis deformans* as found in man and other mammals.

How such anomalies arise is not clearly understood. Alderdice *et al.* (1958) reported that in early developmental stages of chum salmon eggs an oxygen level of 0.4 ppm or less, although not lethal, resulted in the production of monstrosities. Price (1940) showed that the most favourable temperature for the embryonic

development of whitefish was 0.5°C (33°F) and that abnormalities are produced if the developmental temperatures are 6°C (42.8°F) or over. The high frequency of abnormalities in Lake Erie whitefish, and their apparent absence in Heming Lake whitefish, is probably to be accounted for by differences in developmental conditions. The most obvious difference, considering the geographical location of these habitats, might be water temperature during the spawning and incubation period. At Heming Lake the peak of spawning occurs during the latter part of October at about 6°C (43°F). The water temperature rapidly decreases to 0.5°C (33°F), the optimum for development, and remains at that temperature until about the first week in May. The developing eggs are subjected to a relatively constant temperature during embryonic development. In Lake Erie the water temperature decreases later in the season, but the peak of spawning occurs when the temperature is about 6°C (43°F), as in Heming Lake. During the spawning period, however, marked fluctuations in water temperature often occur before the temperature reaches the optimum for development, and the incubation period is probably considerably shorter than at Heming Lake. The high incidence of abnormalities in Lake Erie, as indicated in samples taken in 1948–1949 and again in 1956, may result from unfavourable water temperatures during embryonic development.

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Received for publication November 21, 1960.

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FIG. 1. X-ray photograph of abnormal vertebrae of Lake Erie whitefish.

Biosynthesis of Trimethylammonium Compounds in Aquatic Animals. II. Role of Betaine in the Formation of Trimethylamine Oxide by Lobster (*Homarus americanus*)

The utilization by the American lobster of choline-methyl- C^{14} for the formation of trimethylamine oxide has been described in a previous communication (Bilinski, 1960). Because the oxidation of choline to betaine was also observed, the possibility that this transformation is an intermediate step in the biosynthesis of trimethylamine oxide has been considered. To complete the previous series of experiments, the role of betaine in the formation of trimethylamine oxide has been investigated in lobsters and the present note reports a brief study on the incorporation *in vivo* of radioactive carbon from betaine-methyl- C^{14} into trimethylamine oxide.

Betaine-methyl- C^{14} hydrochloride was prepared from methyl- C^{14} iodide and unlabelled glycine by following the procedure of du Vigneaud *et al.* (1946). Methyl- C^{14} iodide was purchased from Nuclear Chicago Corp. The decomposition of betaine reineckate was, however, not carried out with Ag_2O , as described in the method of du Vigneaud *et al.* The use of a cation exchange resin for conversion of choline reineckate to choline chloride was described recently by Arnstein (1960) and in the present work essentially his procedure was employed for the conversion of betaine reineckate to betaine hydrochloride.

The methods used for the administration of labelled compounds, isolation of trimethylamine oxide and betaine, and determination of the specific radioactivity were described previously (Bilinski, 1960).

Data on the administration of betaine to lobsters and the experimental results are presented in Table I. As indicated in this Table, after administration of betaine-methyl- C^{14} only trace amounts of radioactivity are found in trimethylamine oxide, which has a specific activity 100 to 200 times lower than betaine isolated from lobsters at the end of the two metabolic periods. On the other hand it was found previously (Bilinski, 1960) that after administration of choline-methyl- C^{14} to lobsters the specific activity of trimethylamine oxide amounted

TABLE I. Utilization of betaine-methyl- C^{14} hydrochloride for biosynthesis of trimethylamine oxide in lobsters.

Expt. No.	Weight of lobsters	Metabolic period	Amount administered per 100 g body weight	Specific radioactivity (counts per minute ^a)		
				Betaine		Trimethylamine oxide isolated from lobsters
				Administered to lobsters	Isolated from lobsters	
	<i>grams</i>	<i>hours</i>	μM			
1	495	18	2.65	78,000 ^b	1950	< 10
2	453	42	2.65	78,000 ^b	750	< 10

^aPer infinitely thick planchet (3.8 sq cm) of $BaCO_3$.

^bFor measurement of radioactivity labelled betaine was diluted with a known amount of unlabelled betaine.

to over half of that of betaine. These figures provide no support for the possibility that the oxidation of choline to betaine is an intermediate step in the formation of trimethylamine oxide from choline in lobster.

In connection with this study it might be noted that it has been observed with bacteria that species which produce trimethylamine from choline and acetylcholine have not the ability to convert betaine to trimethylamine (Dyer and Wood, 1947; Campbell and Williams, 1951; Eddy, 1953). Similarly, an enzyme preparation from the leaves of *Chenopodium vulvaria* has been shown to cause the breakdown of choline with liberation of trimethylamine, but not to yield trimethylamine from betaine (Cromwell, 1950). A recent study by Baker and Chaykin (1960) on liver homogenates and subcellular fractions presents further evidence for the presence in animals of an enzyme system capable of oxidizing trimethylamine to trimethylamine oxide.

ACKNOWLEDGMENT

The author is indebted to Dr A. Marcotte for providing aquarium facilities at the Station of Marine Biology, Quebec Department of Fisheries, Grande-Rivière, Que.

Fisheries Research Board of Canada,
Technological Station, Grande-Rivière, Que.

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Received for publication January 4, 1961.

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Decay of Hexachlorocyclohexane in Sea Water

Hexachlorocyclohexane (HCH), more popularly known as benzene hexachloride, has received considerable attention in recent years as an insecticide. It has found effective application in the control of the ambrosia beetle, which attacks fallen logs in the forest and logs on booming grounds. In a study of some of the effects of this insecticide on freshwater and marine fishes, chemical research was instigated to explore its behaviour in sea water.

The instability of the various isomers of HCH to alkali has been described (Slade, 1945). Alkaline dehalogenation of the α and γ isomers in various solvents including water has been reported (Daviaud and Viel, 1952). The reaction under the influence of hot, concentrated, alcoholic alkali is known in detail (Cristol, 1947).

Occurrence of substitution reactions in cold, dilute, weakly alkaline solutions was investigated by several workers and summarized by Ingold (1953, p. 464). Essentially such conditions prevail in the sea and hence a gradual decay of the HCH isomers can be expected. Experiments were conducted to determine the decay rate.

In view of the low solubility of the isomers (Ivanov, 1956), particular care had to be exercised to prepare homogeneous reaction mixtures. A combination of predissolving the substances in diethyl ether, prolonged shaking, filtering, and further diluting proved successful toward this end.

The reaction was allowed to take place at room temperature (*ca.* 20°C) in (a) polyethylene and (b) pyrex glass bottles. The use of polyethylene containers resulted in a more rapid decrease of the apparent HCH concentrations. This may have been caused by adsorption on the polyethylene surface.

The analyses were done by a modification of the method of Hancock and Laws (1955), which is claimed by them to be insensitive to interference by volatile aromatic (presumably also alicyclic) compounds. Its applicability to sea water was tested and confirmed.

Experiments were conducted to test for interference by compounds belonging to groups which could possibly appear as intermediate or end products of the action of sea water on γ -HCH. With several of the compounds a negative test was obtained (Table I).

The α , β and γ isomers are usually all present in commercial HCH-containing insecticides, and if these mixtures are exposed to sea water a differential decay may be expected. Differences in decay rates are shown by the curves presented in Fig. 1. These agree with the reactivity differences observed polarographically (Schwabe, 1953).

Experiments with Millipore-filtered (i.e., nearly sterile) and unfiltered sea water indicate that the reaction is a chemical one and not dependent on the presence of marine organisms.

A comparison of the decay curves for γ -HCH in 50% sea water + 50% distilled water, and in pure sea water, shows that the reaction rate is higher in the latter.

TABLE I. Effect of various compounds on the Hancock and Laws test for hexachlorocyclohexane (HCH).

Group	Compounds tested	Result
Alicyclic chlorides chlorocyclanols cyclanols cyclitols	<i>Trans</i> -1,2-dichlorocyclohexane	Positive (brownish colour)
	<i>Trans</i> -2-chlorocyclohexanol	Positive (brownish colour)
	Cyclohexanol	Negative
	<i>Meso</i> -inositol	Negative
Aromatic chlorides chlorophenols phenols	1,2-Dichlorobenzene	Positive (brownish colour)
	1,2,4-Trichlorobenzene	Positive (brownish colour)
	<i>o</i> -Chlorophenol	Positive (brownish colour)
	Phenol	Negative
	Pyrogallol	Negative

This is as expected inasmuch as the reaction apparently depends on the hydroxyl-ion concentration of the solvent.

Other studies have shown in a week-old reaction mixture the absence of *trans*-1,2-dichlorocyclohexane, *trans*-2-chlorocyclohexanol and the di- tri- and tetra-chlorobenzenes. It remains a question as to what the reaction products are and if they give a positive reaction when subjected to Hancock and Laws'

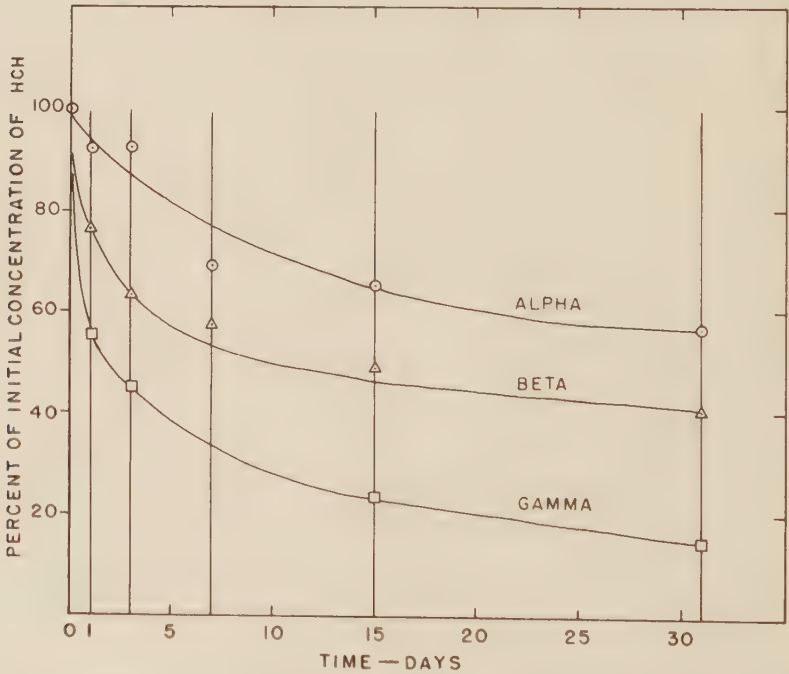


FIG. 1. Decay of isomers of hexachlorocyclohexane (HCH) in sea water. (Polyethylene bottles; coastal sea water.)

procedure. Samples of the reaction mixture showed that even after 12 months of storage (at 20°C) a relatively high apparent γ -HCH concentration remained. It is not possible at present to decide if this is a consequence of stable end products or residual γ -HCH.

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Received for publication January 4, 1961.

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A New Record of the Long-finned Cod, *Antimora rostrata* Gunther, from British Columbia Waters

On August 17, 1960, a rare specimen of the long-finned cod (*Antimora rostrata* Gunther) was caught by Mr M. Hestnes, skipper of the long-liner *Sentinella*, while fishing in waters off the west coast of Vancouver Island. The place of capture was approximately 15 miles southwest of Kyuquot Sound (49°49'N, 127°41'W) and the depth was 250 fathoms.

This is the fourth record from waters adjacent to the British Columbia coast. The three previous specimens were obtained by the *Albatross* expeditions of 1888 and 1890 at Stations 2860 (two) and 3342 (one), respectively, both in the vicinity of the Queen Charlotte Islands (Clemens and Wilby, 1946: 133-134). These early records were obtained from very deep water (876 fathoms and 1588 fathoms, respectively). Likewise, other specimens from other regions of the North Pacific and Atlantic Oceans have been taken in very deep water. The present record is, therefore, somewhat unique in respect to depth of capture.

According to Clemens and Wilby, specimens from the northeastern Pacific Ocean were originally described by T. H. Bean in 1890 as *Antimora microlepis*, a name subsequently considered by Schroeder (1940) to be synonymous with *A. rostrata* Gunther of the Atlantic Ocean. In his monograph of the gadoid fishes of the USSR, Svetovidov (1948: 69) retains the name *A. microlepis* Bean to distinguish the long-finned cod of the North Pacific Ocean.

The present specimen, measuring 38.5 cm in total length, has been deposited in the museum of the Institute of Fisheries at the University of British Columbia.

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Received for publication December 22, 1960.

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Egg Counts of Lake Erie Whitefish

Very little information on the egg numbers of Lake Erie whitefish (*Coregonus clupeaformis*) has been published. The following scanty data may help to fill some of the gaps in the existing knowledge.

During the last week of July and the first week of August, 1948, ovaries of 15 whitefish were removed and preserved in formalin. Total counts were not made but representative samples were taken from several parts of each ovary. These were weighed and the number of eggs in these samples was then counted. The total number was estimated from the ratio of the weight of the eggs sampled to the total weight of the ovary. Connective tissue and blood vessels were removed to minimize extraneous weight that would influence the total count.

Fourteen of the 15 specimens belonged to the 1944 year-class which was so abundant in the commercial catch at that time. The other whitefish belonged to the 1940 year-class.

The counts obtained are shown in Table I.

TABLE I. Egg counts of Lake Erie whitefish captured in 1948.

Year class	Fork length	Weight	Calculated eggs per female
	<i>mm</i>	<i>g</i>	<i>no.</i>
1944	416	...	32,169
"	421	...	40,625
"	424	...	50,050
"	425	...	46,600
"	431	1,205	42,850
"	433	...	40,151
"	439	1,396	41,750
"	444	1,353	51,800
"	449	1,290	40,315
"	453	...	31,105
"	455	1,835	59,500
"	465	1,559	52,450
"	475	1,573	58,200
"	477	1,636	59,906
1940	551	2,891	121,700

The average number of eggs in whitefish of the 1944 year-class was 47,000, while the 8-year-old whitefish had over 100,000 eggs.

With few irregularities, it is apparent that a general relationship exists between size of fish and egg number, i.e., small fish produce fewer eggs than large fish.

Egg diameters were obtained by placing 10 preserved eggs on a millimetre rule and taking the average. The average egg diameter of 13 whitefish ranged from 0.95 mm to 1.40 mm.

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Received for publication January 12, 1961.

Spoilage of Fish in the Vessels at Sea

7. Further Studies on Seasonal Variations in the Landed Quality of Gutted, Trawler-Caught Atlantic Cod and Haddock^{1,2}

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ABSTRACT

The same seasonal variations in the landed quality of trawler-caught Atlantic cod and haddock observed in 1956/57 have been found to occur during similar observations made in 1959.

The poorest quality, at the time of landing, were the fish caught in the summer and in November and early December. The better quality fish were landed during late winter, spring, and early fall.

These results were confirmed by independent observations made on trawler-caught fish at another Nova Scotian fishing port.

INTRODUCTION

THE OBSERVATIONS of experienced plant foremen and trawler fishermen indicate that the landed quality of iced cod and haddock are subject to considerable variation. They also suggest that, in part, these variations in landed quality are associated with the seasons of the year, or with some change in the living fish that occurs at different seasons of the year. Stated briefly, these men believe that they are able to land a much greater proportion of top quality fish during the winter and spring than in the summer and fall.

These observations of the fishermen were confirmed by measurements on the landed quality of trawler-caught cod and haddock during the period December 1956 to the end of December 1957 (Castell *et al.*, 1959). By comparing the quality of fish stowed in the vessels for similar periods, it was found that poorer quality fish were landed during the cold months of November and December and also during the warmer months of June, July and August. The best quality fish were landed during the months of February, March, April and September. This seasonal spoilage pattern was similar for cod and haddock. It was also observed in fish taken from eight individual trawlers as well as from the fleet as a whole.

Immediately the question arises: "Is this seasonal spoilage pattern a constant occurrence, or does it fluctuate or differ from year to year?" During the period March 1959 to January 1960 inclusive, another series of 3170 fish was examined and tested. The fish were taken from the same fleet of trawlers fishing out of Halifax. In this paper the results obtained are compared with the results of the previous series of tests.

¹Received for publication November 9, 1960.

²Part 6 of this series appeared in this JOURNAL, 16(2): 223-233, 1959.

EXPERIMENTAL METHODS

The experimental procedures were similar to those given in the previous paper in this series (Castell *et al.*, 1959). In brief, they were as follows: Large haddock and market cod were picked indiscriminately (except that no fish against the boards were used) from the trawler's pens at the time they were being discharged at the wharf. Ten similar fish were taken from each day's catch. They were filleted immediately, and the fillets were quick frozen in a contact freezer, packed in boxes, and held at -12°C until tested. All trimethylamine (TMA) determinations and the organoleptic grading of the fish were carried out on the defrosted fillets. The method of Dyer (1945, 1950) was used for measuring TMA, except that the extracts used were obtained by grinding whole fillets in a Waring Blendor with twice their weight of water.

In this particular series of tests, a very careful organoleptic examination was carried out on every fillet tested, with the object of assigning a grade based on the extent of deterioration that had taken place. Those fillets with no observable signs of deterioration (off-odours, discoloration, etc.) were graded I. Those that were judged to be merchantable, but not grade I, were classed as grade II. These included fillets with slight off-odours, slight discoloration or other indications of spoilage. Unmerchantable fillets with pronounced or disagreeable signs of deterioration were graded III. Among the 3170 fillets examined, 16 were graded III. As these were not very much worse than some of the poorer quality grade II fillets, it was decided, for statistical purposes, to include them in the grade II group. The result of the grading, therefore, was to divide the fish into grades I and II.

Previous experience had shown that most well-iced fish stowed in the trawlers for 1 to 5 days showed relatively little deterioration. For this reason the fish tested and examined were confined to those that had been iced in the trawlers for 6 to 9 days at the time of landing.

EXPERIMENTAL RESULTS

TRIMETHYLAMINE (TMA) VALUES

TABLE I. Mean TMA values for 6- to 9-day-old gutted cod and haddock, tested immediately after discharge from Atlantic deep-sea trawlers. The first lot of 5110 fish was tested during the period November 1956 to November 1957 inclusive; the second group of 3130 fish was tested during the period March 1959 to January 1960.

Days in ice	No. of fish (1956/1957)	Mean TMA	No. of fish	Mean TMA (1959/1960)
6	2050	1.05	940	0.92
7	1510	1.35	1240	1.34
8	1170	1.90	730	1.77
9	380	2.56	220	2.40

Table I gives the mean TMA values of 6- to 9-day-old fish that were examined during the 1956/57 and 1959/60 test periods. It can be seen that in these two test periods the mean values for fish stowed for the same number of days in ice are quite similar. Figure 1 shows the mean monthly TMA values for the 7- and 8-day-old fish landed in 1956/57 and in 1959/60. The gap in one curve was the result of an insufficient number of tests to give significant results. It can be seen, however, that in general the curves are the same for the two test periods.

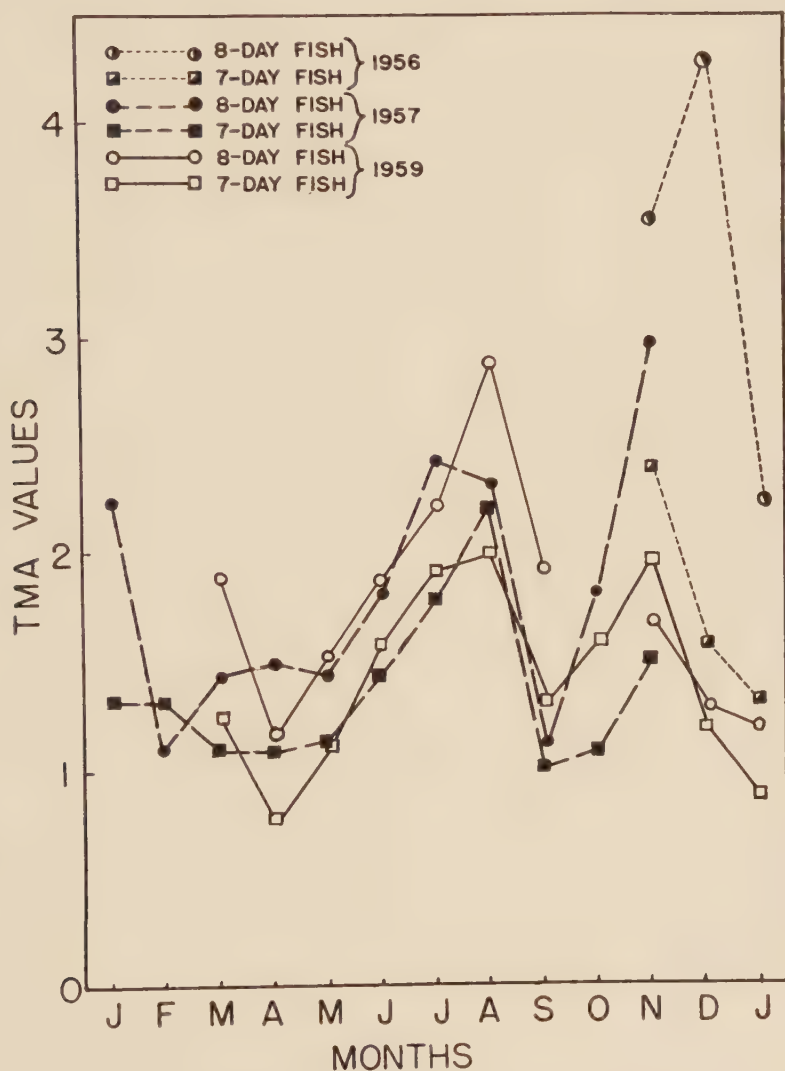


FIG. 1. Mean monthly TMA values of gutted cod and haddock that were iced for 7 and 8 days in the trawler's hold at the time of landing. It can be seen that there is a considerable similarity in the general slope of the curves for the different years.

The curve for the 7-day-old fish is probably the most representative, as it is based on a larger number of fish than those from the other storage-age categories, and they are a little more evenly distributed throughout the year. Further details showing the range and distribution of the TMA values for the 7-day-old fish

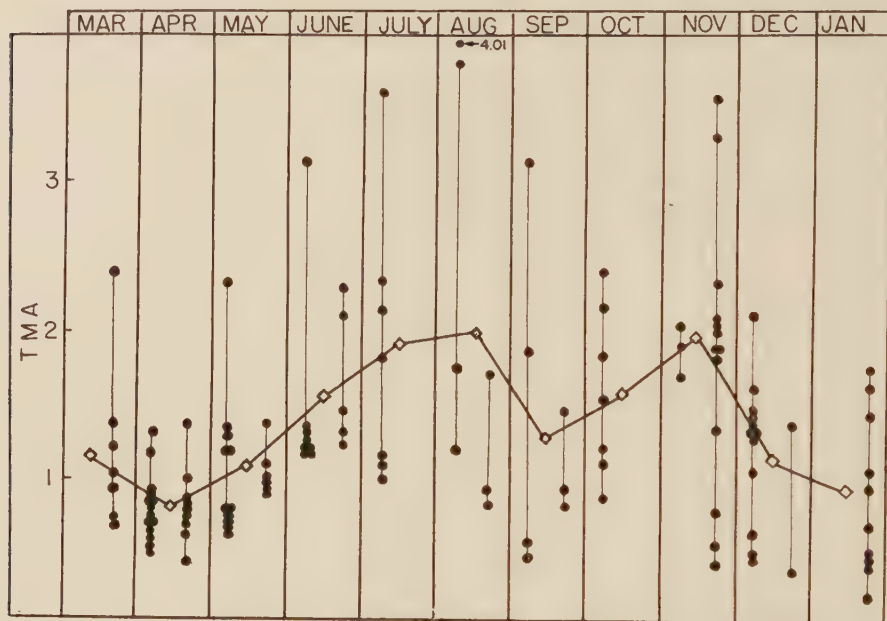


FIG. 2. Distribution of the TMA values for individual catches of 7-day-old fish, recorded at fortnightly intervals. The horizontal curve shows the mean monthly values for the same fish. During the spring months the individual values are grouped more closely around the means.

are given in Fig. 2, which shows the mean monthly TMA values and the scatter about the means for the individual catches taken at fortnightly intervals. Each individual point on the half-monthly vertical lines is a mean TMA value for one group of ten similar fish taken from one pen, representing a day's catch. In almost every month one or two trawlers had a "bad" trip, resulting in poorer quality fish with much higher than average TMA values. It can be seen that during March, April, May, and the first half of June, the values for the individual catches were more closely grouped around the monthly means. The higher average values during the summer and most of the fall were accompanied by a wider spread in the values for the individual catches.

This graphic picture showing the distribution of the TMA values at different seasons can be expressed more precisely: the mean value for all 7-day-old fish caught during March, April and May is 0.95, with a standard deviation of 0.41.

For the period of June, July and August both the mean and the standard deviation are approximately doubled, being 1.80 and 0.90 respectively.

ORGANOLEPTIC GRADING

Up to this point, the criterion used for indicating the degree of spoilage has been the accumulation of TMA in the muscle. In addition to this, an organoleptic grade was given to every fillet tested. Figure 3 compares the monthly percentages of grade I and grade II fish with the monthly mean TMA values. As might be expected, when the TMA values rose, the percentage of grade I fish decreased. The overall seasonal spoilage pattern obtained from measuring TMA was similar to that obtained by organoleptic grading of the fillets.

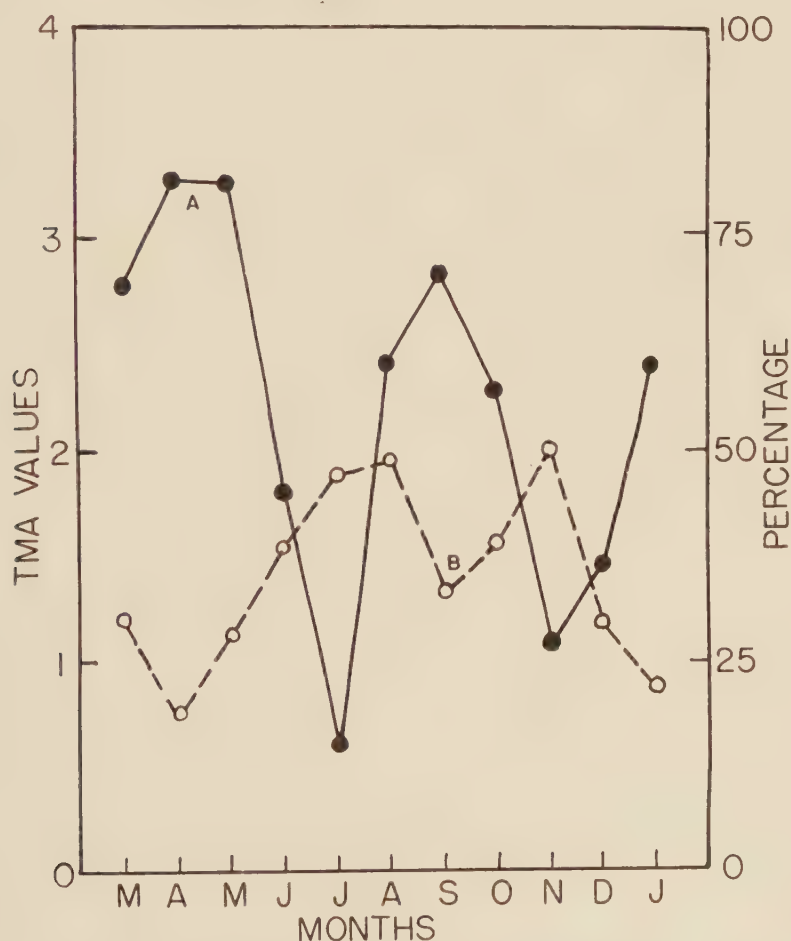


FIG. 3. Mean TMA values (B) and the percentage of grade I fish (A) for 7-day-old fish examined during the 1959/60 test period.

Results from Lunenburg. While this second series of tests was being carried out with fish landed at Halifax, the Lunenburg Sea Products Ltd., Lunenburg, N.S., was independently carrying out a somewhat similar series of 2400 tests with trawler-caught fish landed by other vessels at the fishing port of Lunenburg.

Their method of selecting the fish to be tested was not the same as that used in our tests. It tended to stress the poorer quality fish landed by their trawlers, rather than a random selection from specific storage-age groups. Nevertheless it can be seen from Fig. 4 that the seasonal changes in quality observed at Lunenburg coincide with those observed at Halifax.

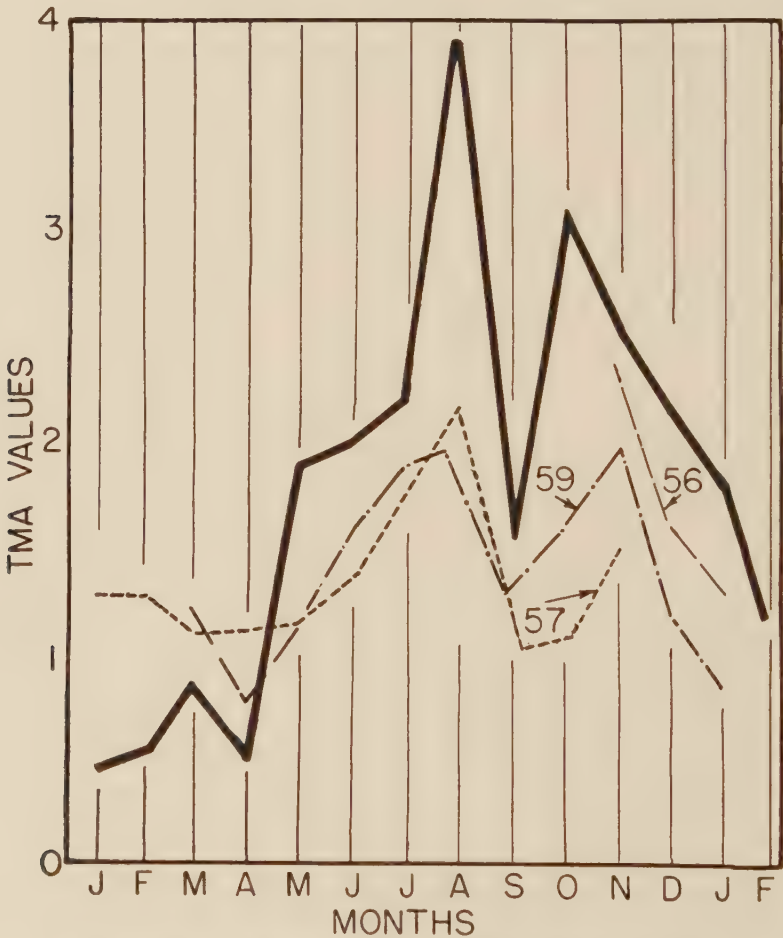


FIG. 4. Monthly mean TMA values (heavy line) for the 2400 fish tested at Lunenburg (see text for details) compared with similar TMA-value curves for the 7-day-old fish tested in Halifax during portions of 1956, 1957 and 1959.

It is also of interest to read the summation of the results of their observations on the seasonal changes in the quality of the cod and haddock landed in Lunenburg during 1959:

"The year 1959 can be divided into three parts (in regard to the quality of the fish landings) namely: 1) January to April—a time of top quality fish when all boats are landing high percentages of cod and haddock; 2) May to August—a time of poorer quality fish, when some boats are landing large catches of flounder and redfish (and therefore less cod and haddock); 3) September to December—the quality during September is fairly well up. There is a sharp drop in October and a rise again in December."

CONCLUSIONS

Comparison of the landed quality of gutted cod and haddock in 1959 and part of 1960 has shown the same seasonal fluctuations that were previously observed in 1956/57. Better quality fish are landed during the late winter, spring, and early fall than during summer and late fall. A similar pattern was obtained by independent observations made in another fishing port during 1959. This strongly suggests that the pattern observed is a normal occurrence and can be expected to repeat itself under similar conditions.

Examination of the data from individual catches shows that during seasons of relatively poor quality landings, the increase in mean TMA values is accompanied by an increase in the standard deviation. This indicates that in spite of the drop in the quality of the fish as a whole, some vessels are also landing comparatively good fish.

Seasonal fluctuations in the quality of the landed fish, observed by using TMA values, were confirmed by careful organoleptic grading of the fillets.

From a commercial standpoint it is interesting to note the changes in the percentage of grade I fish landed at different periods of the year. During the late winter and spring months, approximately 75% of the fillets cut from the 7-day-old fish were free from off-odours and were graded I. During the warm summer months, and again in November, the amount of grade I 7-day-old fish dropped to 25% or less.

In addition to the fact that seasonal changes occur in the spoilage pattern of these fish, there is also the more fundamental problem of establishing the cause or causes of these changes. Speculation on these causes was given in the previous paper of this series (Castell *et al.*, 1959). No additional information has been obtained that would lead to any firmer conclusions than the suggestions given there.

Note. In an accompanying paper Castell *et al.* (1961) describe results of a further study on the relation between TMA values and the organoleptic grades given to these same fish. It was found that during the summer and late fall, fillets with a given TMA level had a lower organoleptic rating than fillets with the same TMA level caught in the spring or late fall. This does not alter the overall picture of the seasonal variations in the landed quality of the fish that have been recorded here. However, it does indicate that if the TMA values were to be transposed to corresponding organoleptic ratings, many of the fish caught in summer and late fall would be even poorer in quality than the observed rise in the TMA values would indicate.

ACKNOWLEDGMENT

This work could not have been done without the co-operation of the management and staff of the Sea-Seald Division of the National Sea Products Ltd. at Halifax. For this we are sincerely grateful.

We also wish to express our thanks to F. C. Read, chemist, and to the management, of Lunenburg Sea Products Ltd., Lunenburg, N.S., for granting us permission to include in this paper the results of the tests made at that plant.

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Grading Fish for Quality

4. Variations in the Relation Between Trimethylamine Values and Grades for Gutted, Trawler-Caught Atlantic Cod and Haddock^{1,2}

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ABSTRACT

The accuracy of the trimethylamine (TMA) grade probability curve, developed in 1958 by Hoogland for gutted, trawler-caught Atlantic cod and haddock has been verified by tests made on 3170 cod and haddock.

It has also been shown that the relation between TMA and grade is not the same for cod as it is for haddock. For a given TMA level, haddock show greater deterioration.

The relation between grade and TMA also changes with the season. For a given level of TMA, fish caught in the summer and late fall usually show more deterioration than those caught during the spring months.

INTRODUCTION

DURING PREVIOUS STUDIES on the grading of fish, Hoogland (1958) developed a probability curve showing the relation between organoleptic grade and trimethylamine (TMA) values for gutted, trawler-caught Atlantic cod and haddock. This was based on data obtained from grading of several hundred fish carried out at this Station by a group of experienced fish-plant foremen. Since that time we have had occasion to grade and to make TMA determinations on fillets cut from an additional 3170 fish.

The data, obtained from grading and testing this large number of fillets cut from fish taken directly out of the trawlers, have provided an opportunity of verifying the curve developed by Hoogland. Because the species and the date of landing for each fish had been recorded, it was possible to develop separate curves showing the TMA-grade relations of cod and haddock separately, as well as for fish caught at different seasons of the year.

EXPERIMENTAL PROCEDURES

Large haddock (3 to 7 lb) and market cod (3 to 8 lb) were all taken from the trawlers at the time of unloading at the wharf. Within a very short time the fillets were removed by experienced cutters, frozen in a contact-type quick freezer, and delivered to this Station by truck, where they were held in frozen storage until tested. This procedure was followed to prevent deterioration of the fillets between the time the fish were removed from the trawler and the fillets were tested.

Storage in the freezer was limited to the shortest time compatible with the time schedule for testing. Usually this was from 1 to 48 hours. At certain

¹Received for publication November 10, 1960.

²Part 3 of this series appeared in this JOURNAL, 15(4): 729-748, 1958.

periods, however, when large numbers of fish were being recovered, the storage of some fillets was extended up to but never beyond 14 days. Control tests showed that fillets stored under these conditions showed no significant change in weight or TMA values at 14 days.

Before testing, the fillets were thawed by leaving them at room temperature in waxed cardboard boxes. During this stage, and particularly when the last traces of frost were leaving, the fillets were repeatedly examined and smelled by at least two, and more often three persons in the laboratory who had had considerable experience in grading fillets. Because of the conditions under which the fish had been selected there were very few spoiled, i.e. grade III, fish. The problem of grading was chiefly one of determining whether the fillets showed no observable deterioration (grade I) or were in the early stages of spoilage where the first off-odours were beginning to develop grade II.

The TMA determinations were always made by grinding the whole fillets with twice their weight of water in a gallon-size Waring Blendor and then testing by the colorimetric procedures given by Dyer (1945, 1950).

Table I condenses the TMA values and the grading results of all the fish tested. It is given both to present a general picture of the results obtained and also to show the procedure used to develop the curves relating TMA values to

TABLE I. Percentage of fillets in grades I and II in various TMA ranges between 1.0 and 10.0, for both cod and haddock, taken over the 11-month test period.

TMA ranges	Number of fillets			Percentages	
	Grade I	Grade II	Total	Grade I	Grade II
0.00-0.40	409	92	501 (263)*	82	18
0.41-0.60	302	80	382 (207)	79	21
0.61-0.80	258	98	356 (171)	72	28
0.81-1.00	241	136	377 (197)	64	36
1.01-1.20	152	136	288 (125)	53	47
1.21-1.40	104	129	233 (90)	45	55
1.41-1.60	92	117	209 (94)	44	56
1.61-1.80	53	107	160 (71)	33	67
1.81-2.00	46	102	148 (95)	31	69
2.01-2.20	27	68	95 (52)	28	72
2.21-2.40	20	63	83 (39)	24	76
2.41-2.60	15	65	80 (37)	19	81
2.61-2.80	8	42	50 (27)	16	84
2.81-3.00	5	38	43 (27)	12	88
3.01-3.20	6	21	27 (12)	22	78
3.21-3.40	2	18	20 (9)	10	90
3.41-3.60	3	13	16 (12)	19	81
3.61-3.80	1	18	19 (10)	5	95
3.81-4.00	2	12	14 (7)	14	86
4.01-5.00	2	34	36 (22)	5	95
5.01-6.00	3	20	23 (9)	13	87
6.01-7.00	0	6	6 (1)	0	100
7.01-8.00	0	3	3 (2)	0	100
8.01-9.00	0	0	0 (0)	0	...
9.01-10.00	0	1	1 (0)	0	100

*Figures in parentheses refer to numbers of haddock only.

the percentage of fish in each of the grades. This same procedure has been used for treating the results obtained from the cod and haddock separately as well as for fish taken at the different seasons of the year. In addition to the total numbers of cod and haddock in each of the TMA ranges (column 4 of the Table) an additional set of figures has been added in parentheses. This is the number of haddock only. From this it can be seen that in each of the TMA ranges there were approximately equal numbers of cod and haddock.

Figure 1 shows the TMA-grade probability curve developed by Hoogland (1958) for mixed, gutted, trawler-caught cod and haddock taken throughout the fishing season. Superimposed upon this curve are the results obtained

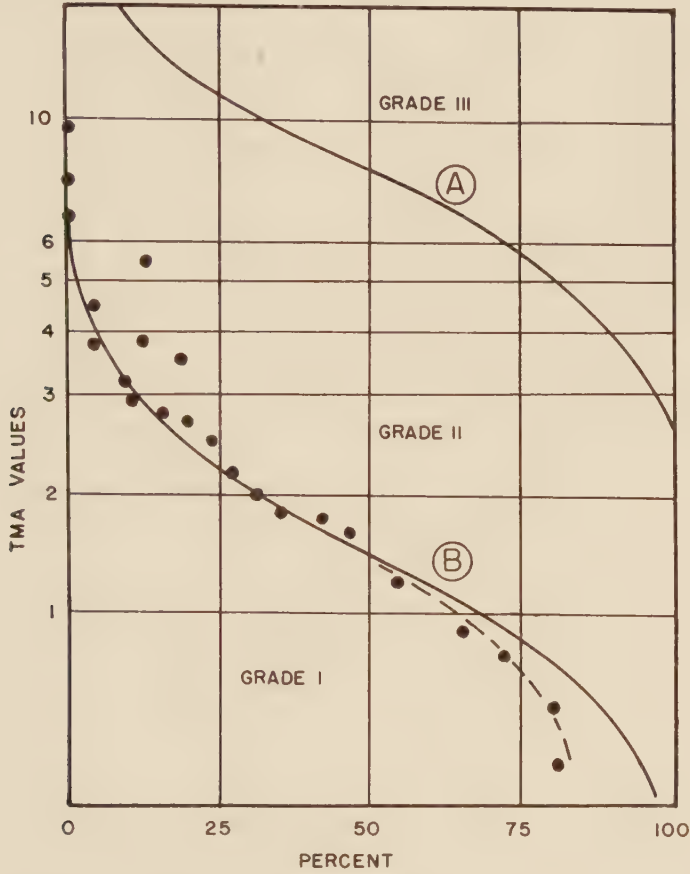


FIG. 1. "A" and "B" are the probability curves developed by Hoogland, showing the relation between TMA values and grades for gutted, trawler-caught Atlantic cod and haddock. The black circles show TMA values and percentage distribution in grades I and II for 3170 6- to 9-day-old cod and haddock. The number of observations represented by each of these points is shown in column 4 of Table I.

from 3170 mixed cod and haddock that were tested and graded in the period March 1959 to the end of January 1960. It can be seen that they follow very closely along the curve developed by Hoogland.

The curve in Fig. 1 is based on the combined results of 1581 tests made on fillets from haddock and 1589 tests made on fillets from cod. These, in turn, can be subdivided into:

Haddock:	grade I — 750;	grade II — 831
Cod:	grade I — 1001;	grade II — 588.

This shows a fairly even distribution, both in regard to species and to grades in the fish that were examined. Figure 2 separates the results obtained from the cod and the haddock, and includes Hoogland's curve as a reference. It

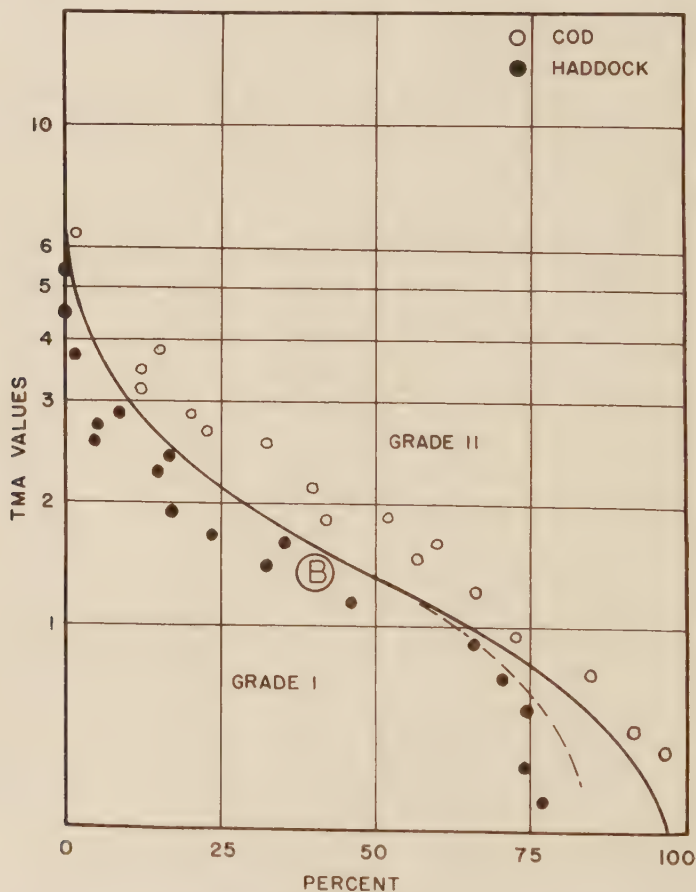


FIG. 2. "B" is Hoogland's probability curve showing the relation between TMA values and grades for mixed cod and haddock. The data points surrounding this curve were obtained from the same fish that were used in Fig. 1, except that the cod and haddock have been treated separately.

is very obvious that haddock were down-graded at lower TMA levels than cod. For example, at a TMA level of 1.0, only 55% of the haddock were grade I, while at the same level close to 70% of the cod were grade I.

It has been shown previously that the spoilage pattern of these trawler-caught Atlantic cod and haddock was not the same throughout the year. At the time of landing, the winter, spring and early fall fish were in a better state of preservation than the corresponding fish caught in the summer and late fall months (Castell *et al.*, 1959; Castell and Giles, 1961). In addition to affecting the rate of spoilage, there probably were also slight differences in the course of spoilage at different periods of the fishing season. This leads one to question whether a given TMA value has the same significance, in terms of the extent of spoilage that has occurred, at different seasons of the year.

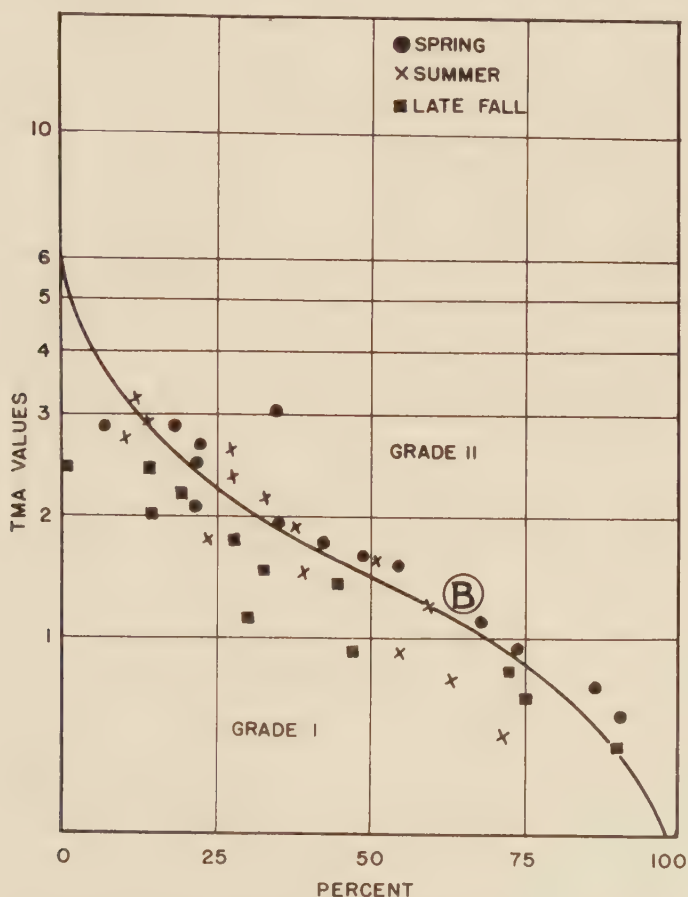


FIG. 3. "B" is Hoogland's probability curve showing the relation between TMA values and grades for mixed cod and haddock. The data points surrounding this curve were obtained from the same fish as those used in Fig. 1, except that the fish caught in the spring, in the summer, and in the late fall have been treated separately.

Again using Hoogland's curve as a background, the TMA-grade relations for mixed cod and haddock have been compared for fish landed in the spring, summer and late fall.

It can be seen from Fig. 3 that fish caught at different seasons of the year did not have the same TMA-grade relation. During the spring, when larger catches and better quality fish were being landed, a given TMA level indicated a higher quality fish than the same level for the similar fish caught in the summer or late fall.

It is interesting to observe what happens when the effects of species and season on the TMA-grade relation are combined. This is illustrated in Fig. 4

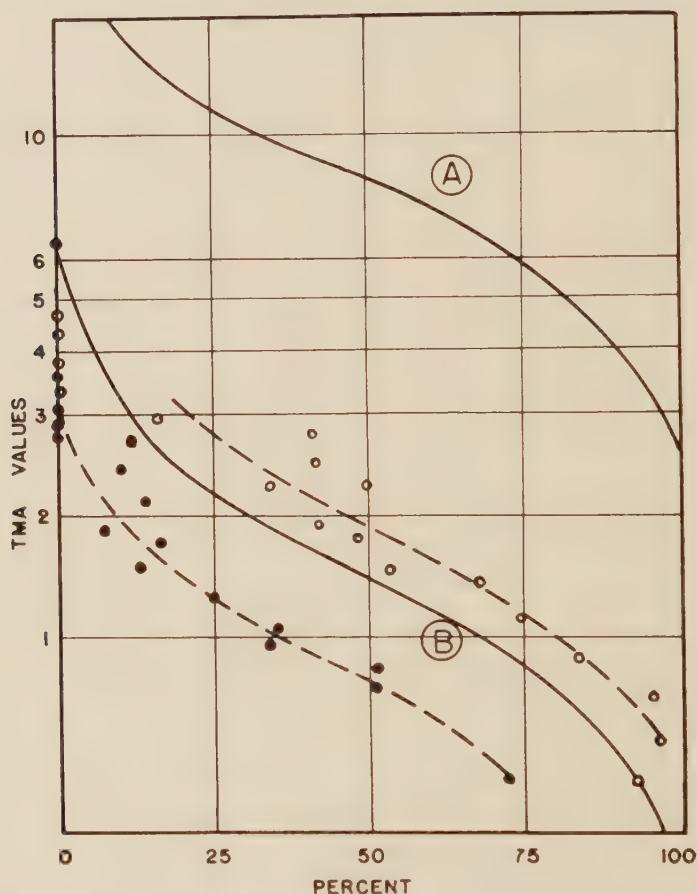


FIG. 4. TMA values and the percentage distribution in grades I and II for cod caught in the spring (open circles) and haddock caught in the summer (closed circles). These fish were all trawler caught and were in ice from 6 to 9 days at the time of landing. Hoogland's curve "B" is added to the Figure for reference and comparison.

which gives the data for cod, caught in the spring, with haddock, caught in the summer. Under these conditions it can be seen that haddock with a TMA value of 1.0 would have about 35 chances out of 100 of being grade I while a cod with the same TMA level would have 80 chances in 100 of being grade I.

DISCUSSION OF RESULTS

This seasonal shifting relation between grade and TMA value apparently complicates the problem of obtaining an objective measurement for the quality of fish. But in point of fact, after examining these results, the fishery officers, who had been continuously grading fish on the wharf, have been emphatic in their reaction: "This certainly clarifies the problem for us and demonstrates what we already know to be so!"

It also underlines the suggestion that "Although objective measurements can often be very useful as references, they should not be used as the bases for defining commercial grades of fish."

It might be objected that all the results given in this paper deal only with strictly fresh fish or those in the very early stages of spoilage. No data are presented to verify the other line in Hoogland's TMA-grade probability curves—that is, the line separating grades II and III. This is a justifiable criticism and it would have been of real interest to see what happened to these same relationships during the later stages of spoilage.

This occurred simply because too few grade III fish were encountered among those that were tested to give results that would have meaning.

One other point is worth mentioning. The TMA-grade relations that were found for the mixed cod and haddock during the whole test period, agree very well with the probability curve developed by Hoogland (Fig. 1). There is one small portion, however, where they do not agree. This is in the region of the very low TMA values at the lower, right-hand end of the curves. Hoogland's curve indicates that there should have been greater percentages of grade I fish than were actually found. If the fish that were tested had included some that were 1 to 3 days in ice, this difference would not have occurred, since a higher percentage of very fresh fish with low TMA values will be graded I than would be found with 6- to 9-day-old fish with similar low TMA values.

It would seem very probable that for unselected fish, taken indiscriminately from the trawler's catch, this region of Hoogland's curve gives the truer picture. It also indicates the care that is needed in applying a probability curve to a specifically selected group of fish such as these older cod and haddock with very low TMA values.

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Surface Temperature and Salinity off the Washington and British Columbia Coasts, August, 1958 and 1959¹

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ABSTRACT

Oceanographic data collected off the Washington and British Columbia coasts during August, 1958 and 1959, through Canadian and United States research programs provide the best synoptic coverage attained in this area. Comparison of August surface data for the two years shows that the effects of local runoff can be traced over several hundred miles offshore. This implies, but does not necessarily confirm, the absence of any appreciable net surface current parallel to the coast northward of the Strait of Juan de Fuca to Dixon Entrance, in summer.

The 1958 observations were made at the time of the anomalous Fraser River sockeye run through Johnstone Strait and provide a good picture of the existing coastal and offshore oceanographic conditions. It is suggested that the seaward extent of dilute surface water may determine the location where homeward migrating salmon enter coastal waters.

INTRODUCTION

SOCKEYE SALMON (*Oncorhynchus nerka*) returning to spawn in the Fraser River, British Columbia, have a choice of two routes around Vancouver Island, from the north through Johnstone Strait or from the south through the Strait of Juan de Fuca. The latter is considered the normal route, but in 1958 practically the entire run was reported to have approached Vancouver Island from the north, and an unprecedented percentage of an unusually large run proceeded through Johnstone Strait (Internat. Pacific Salmon Fish. Comm., 1959).

This behaviour may have been due to a progressive northward intrusion of warm water off the Canadian coast from 1955 to 1958 as shown on the sigma-*t* surface 26.60 by Tully *et al.* (1960).

Alternatively, it could be due to an unusual change in position or extent of the local runoff flowing out of Queen Charlotte Sound and the Strait of Juan de Fuca. The migration pattern of the Fraser River salmon run returned to normal in 1959 (Internat. Pacific Salmon Fish. Comm., 1960). The purpose of this report is to present the surface conditions off the Washington and British Columbia coasts during August, 1958 and 1959, and to determine if any significant differences occurred in these two years that could have affected the 1958 migration route of the salmon.

Barnes and Paquette (1954) have described the general circulation off the Washington coast and noted that the brackish water originating in the outflow

¹Received for publication December 5, 1960.

of the Columbia River could be detected over 200 miles offshore. Doe (1955), presenting data from project "Offshore", has described the origin and identification of water masses off the British Columbia coast, and detected brackish water several hundred miles offshore which he believed originated in local runoff.

SURFACE DATA, 1958

At the time the Fraser River salmon run was entering coastal waters in 1958, there were numerous oceanographic cruises being conducted in the area. The M.V. *Attu* and M.V. *Pioneer*, chartered by the Seattle Biological Laboratory of the U.S. Bureau of Commercial Fisheries to conduct experimental fishing and oceanographic research for the International North Pacific Fisheries Commission, were returning to Seattle, having completed operations in the Aleutian area (Favorite and Pedersen, 1959). At the same time, the Pacific Oceanographic Group of the Fisheries Research Board of Canada was making observations from C.N.A.V. *Whitethroat* and C.N.A.V. *Oshawa* (Fisheries Research Board of Canada, 1958 a, b). Also, the Oceanographic Laboratories of the University of Washington, Seattle, Washington, were independently conducting an oceanographic cruise in R.V. *Brown Bear* (Fleming *et al.*, 1959). Figure 1 shows the locations of all surface observations made from these vessels in the area under consideration during August 1958. The observed surface salinity and temperature distributions are shown in Fig. 2.

TEMPERATURE

The temperature distribution (Fig. 2) shows three interesting features: The region of divergence of the isotherms in the vicinity of Lat. 50°N , Long. 135°W ; the band of cool water along the coast; and the apparent northward intrusion of warm water seaward of the cold water along the coast.

The divergence of the isotherms appears to be associated with a tongue of dilute water extending seaward, and is not to be confused with the divergence of the Westwind Drift which occurs farther offshore. The band of cold temperatures along the coast has been explained by Tully (1937) and Barnes and Paquette (1954) as a normal late summer condition, and has been attributed to upwelling.

Reference is made only to the August, 1950 and 1951, data presented by Doe (1955) and the average August conditions presented by Robinson (1957) in determining whether or not the 1958 conditions were anomalous. Although limited data are available for other years, only the above data are considered to be adequate enough to permit comparison. The 1951 temperatures are representative of average conditions and the 1958 temperatures were approximately 1 to 2°C higher than average; however, the general configuration of the isotherms was similar.

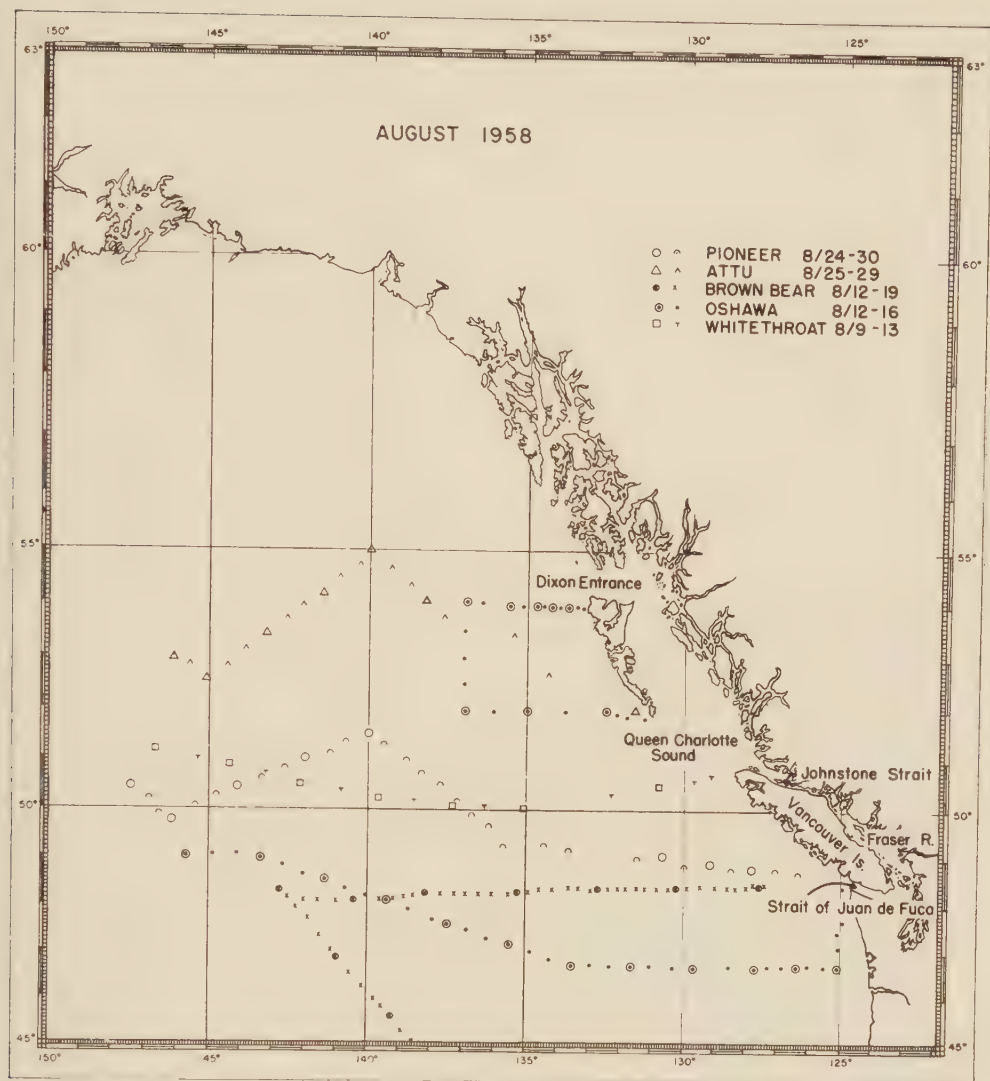


FIG. 1. Oceanographic and bathythermograph stations, August 1958.
 (Large symbols indicate oceanographic stations).

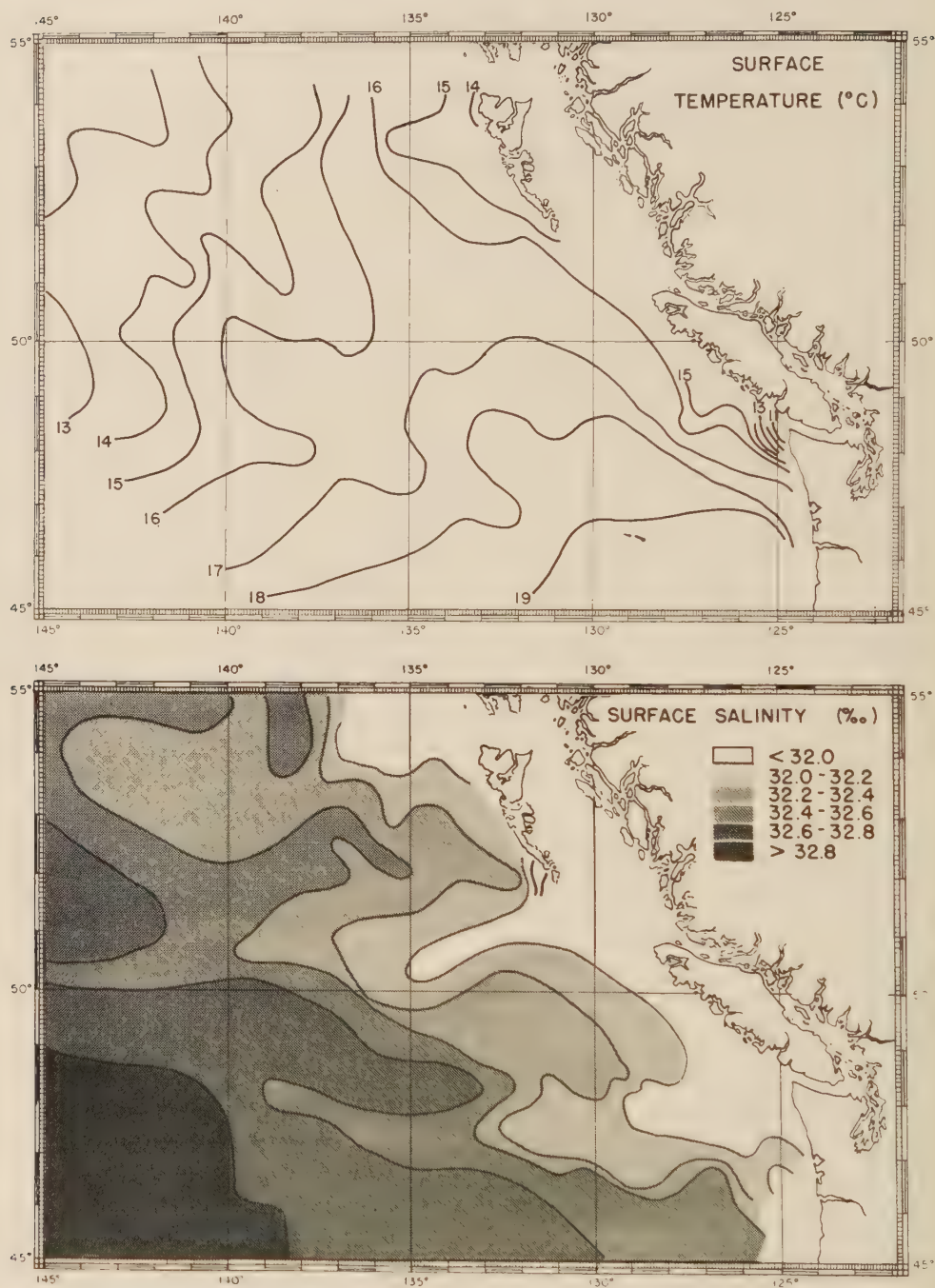


FIG. 2. Surface temperature and salinity, August 1958.

SALINITY

The effects of local runoff from the Strait of Juan de Fuca, Queen Charlotte Sound, and Dixon Entrance are immediately apparent as excursions of dilute water into the coastal and offshore regions. These occur as three distinct tongues normal to the coast, and can be identified several hundred miles offshore. The protrusion of the 32.0‰ isohaline off Queen Charlotte Sound extended to Lat. 50°N and Long. 135°W, coinciding with the divergence of the isotherms, as noted above.

SURFACE DATA, 1959

The 1958 data showed that closely spaced observations are necessary to show continuity of the properties in the coastal region. Having been notified of the extensive 1959 summer cruise plans of the Pacific Oceanographic Group (Fisheries Research Board of Canada, 1959), personnel aboard the charter vessels *Pioneer* and *Tordenskjold* made additional observations along Lat. 51 and 53°N in August 1959 while en route to Seattle from the Aleutian area (Favorite *et al.*, 1961). Bad weather prevented taking as many observations as were planned. Figure 3 shows the locations of the surface observations, and the temperature and salinity distributions are shown in Fig. 4.

TEMPERATURE

The surface temperatures in 1959 were generally 2 to 3 C° less than in the previous year, and approximately 1 C° less than the average conditions shown by Robinson (1957). The offshore divergence of the isotherms occurred a little southward and nearer to the coast than in 1958. Even though a marked difference existed in the surface temperatures, the general configuration of the isotherms was similar to that of August 1958. The band of colder temperatures was again present along the coast, and the apparent northward intrusion of warm water was evident approximately 200 miles west of the Washington coast, but did not intrude northward past Vancouver Island as it did during the previous year.

SALINITY

As in August 1958, the local dilution from Queen Charlotte Sound and Dixon Entrance was clearly evident off the coast, but the region of dilute water was confined nearer the coast along a front extending from Lat. 49 to 55°N about 300 miles offshore and approximately parallel to the coastline. Doe (1955) denoted this general area as the separation of the coastal and offshore water masses.

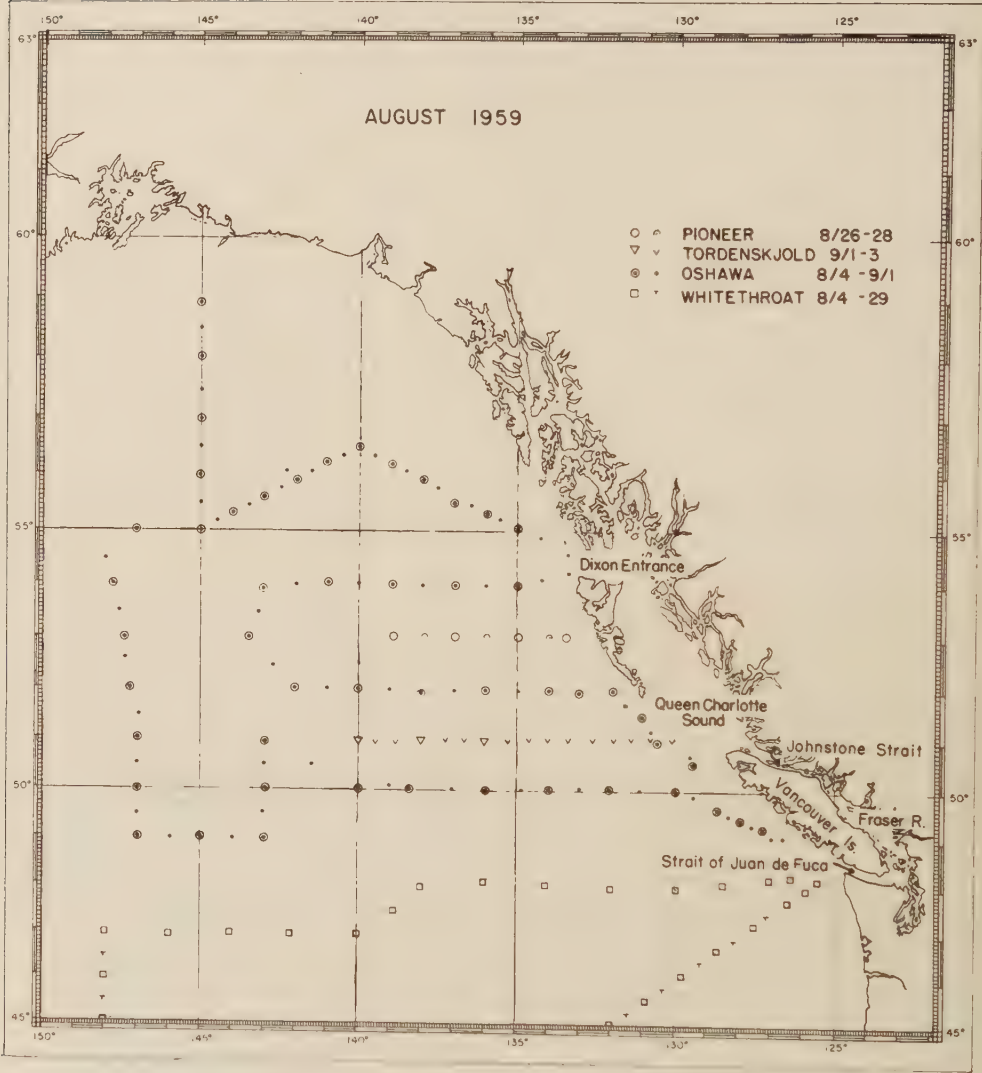


FIG. 3. Oceanographic and bathythermograph stations, August 1959.
(Large symbols indicate oceanographic stations.)



FIG. 4. Surface temperature and salinity, August 1959.

DISCUSSION AND SUMMARY

The coasts of Washington and British Columbia are mountainous, and snow-melt and precipitation draining in spring from an extensive watershed area result in the discharge of considerable amounts of fresh water into the coastal regions. After mixing with sea water in the inshore area, the runoff enters the ocean directly or through various straits or passes. An estimate of how far offshore the properties associated with the runoff may be present, can be ascertained by tracing the seaward extent of the coastal dilution as shown by the surface salinity.

The local runoff from Queen Charlotte Sound in August 1958, as shown in Fig. 2, can be traced across the coastal region into the offshore region, and existed several hundred miles further offshore than shown by previous data cited. Surface temperatures were approximately 1 to 2 C° greater than average. In 1959, although the runoff again was clearly evident offshore, it was confined nearer to the coast than in 1958. Surface temperatures were 2 to 3 C° less than in 1958, and approximately 1 C° less than average.

In both years it is apparent that the surface temperature is not a good indicator of the extent of location of the local runoff during summer. This may possibly be explained by the fact that the cold, snow-melt runoff enters the ocean in late spring; thus subsequent insolation during the summer would result in an equilibrium ocean temperature which prevents any further thermal identity of the water. This gradual warming would tend also to stabilize the layer of dilute water and help to maintain the identity of its salinity values.

In order to ascertain whether the temperature or the salinity more clearly reflected the surface circulation, the dynamic topography of the area was investigated. However, the limited number of stations providing data suitable for permitting this calculation, in contrast to the number of surface observations available, prevents a comparative picture. A similar lack of correlation between the surface temperature and salinity distribution appeared in Doe's work. He compared also the dynamic topography to isentropic charts and discovered that considerable difference in detail existed.

Then too, the excursion of the local runoff, as clearly defined tongues normal to the coast, is interesting because it suggests the absence of any appreciable northerly or southerly current along the coast north of the Strait of Juan de Fuca to Dixon Entrance during the summer months. This is not confirmed by calculations of water transport, and the discrepancy can be resolved only by future direct current measurements.

In attempting to relate surface conditions in the ocean to the migration of salmon, one must be very cautious, because the factors which guide anadromous species to their parent streams after a 1- to 3-year residence in the ocean are not known (Talbot and Sykes, 1958).

The similarity between the location and seaward extent of the local dilution from the British Columbia and Washington coasts in August, 1958 and 1959, and the lack of knowledge concerning the response of salmon to variations in the

marine environment, prevent one from making any specific conclusions in regard to the effect of oceanographic conditions on the anomalous migration path of the 1958 Fraser River salmon run. Nevertheless, the extrusions of dilute surface water off the British Columbia coast provide an indication of the location in the ocean where the shoreward-migrating salmon first detect this dilution and may determine the point at which they enter the coastal waters.

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Observations on *Post mortem* Biochemical Changes in Fish Muscle in Relation to *Rigor mortis*¹

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ABSTRACT

The influence of the degree of exhaustion of fish at death and their subsequent storage temperature on the relationship between *rigor mortis*, lactic acid formation and changes in certain acid-soluble phosphorus-containing fractions in muscle have been examined. The fish used were rainbow trout (*Salmo gairdneri*) and starry flounders (*Platichthys stellatus*) killed under controlled conditions in an aquarium and sockeye salmon (*Oncorhynchus nerka*) caught by gill net or seine net under commercial conditions. The majority of the fish contained little or no molybdate-labile P (phosphocreatine) at death, but in those that did (chiefly unexercised fish) the P of this fraction, sometimes after a short period of increase *post mortem*, decreased to a very low value. Acid-labile P (adenosine-triphosphate) decreased later *post mortem* than did phosphocreatine, and rigor developed during this period of decrease. Onset of rigor was detected at higher concentrations of acid-labile P at 20 than at 0°C. Acid-stable P decreased *post mortem*, but without showing the rather sudden disappearance from the muscle exhibited by the two labile fractions, the decrease continuing throughout rigor.

In unexercised fish the relationship between the course of rigor and lactic acid formation was distinctly different at 0 and 20°C. At 20°C the lactic acid concentration reached a maximum in the muscle by the time rigor was fully established or very soon thereafter. At 0°C accumulation was much slower and had only reached about 50% of its maximum concentration when rigor was fully established. Evidence was presented that the duration of full rigor is related to the continued production of lactic acid in the muscle, rather than to the quantity of lactic acid accumulated.

INTRODUCTION

EXCELLENT DESCRIPTIONS of *rigor mortis* in fish, including observations of the effects of several variables on the time course of rigor, were published years ago (Ewart, 1887; Anderson, 1909). Since then numerous investigations have been made of the biochemical changes that occur in fish muscle within a few hours or days *post mortem*, but in only a few of these investigations have attempts been made to relate the changes to the course of *rigor mortis*.

Leim *et al.* (1927), Macleod and Simpson (1927), Ritchie (1927), Macpherson (1932), Sharp (1934), Locke (1935), Amano *et al.*, (1953), and Noguchi and Yamamoto (1955a, b) have studied the changes in glycogen and lactic acid content of fish muscle *post mortem*. Macleod and Simpson (1927) and Ritchie (1927) made observations of the relation between the changes and the course of

¹Received for publication January 13, 1961.

rigor mortis. Ritchie found that while there was some increase in lactic acid concentration during rigor, there was little or none once rigor had disappeared and the findings of Macleod and Simpson tended to confirm this. Locke (1935) found that fish caught in the spawning season either failed to go into *rigor mortis* at all, or stayed in rigor for only a very short time. The quantity of lactic acid accumulated in spawning fish *post mortem* was abnormally low and did not at any time reach values found in non-spawning fish in good condition. Although Macleod and Simpson concluded that rigor can never become marked so long as glycogen remains in the muscle, the later findings of Macpherson (1932), Sharp (1934), Tarr (1949), and Noguchi and Yamamoto (1955a, b) indicate that this is not true, but rather that some might still be present during rigor, depending on the quantity of glycogen present at death and on the subsequent storage temperature.

Sharp (1931), Fujimaki and Kojo (1953), Heen (1954) and Saito and Arai (1957a) examined the changes that occurred in the concentration of phosphocreatine (molybdate-labile phosphorus) in fish muscle *post mortem*, and found that it decreased rapidly from the time of death. Fujimaki and Kojo (1953) reported that phosphocreatine disappeared from the muscle before full rigor was established. They also examined the changes that occurred in the acid-soluble phosphorus compounds of fish muscle during the first 8 hours *post mortem*, and found that the major change was a decrease in nucleotide phosphorus and in glucose-6-phosphate. Golovkin and Pershina (1957) investigated the changes that occurred in the acid-labile phosphorus of fish muscle at intervals of 1 or 2 days for a period of 10 days *post mortem*. Noguchi and Yamamoto (1955a) found that acid-labile phosphorus disappeared from fish muscle before *rigor mortis* was fully established. Jones and Murray (1957), Murray and Jones (1958), and Saito *et al.* (1957b, 1959a, b) made a detailed examination of the *post-mortem* changes in the nucleotides of fish muscle but the relation between these changes and the course of *rigor mortis* was not recorded.

In the present work we have investigated the influence of the degree of exhaustion of fish at the time of death and of the subsequent storage temperature on the course of *rigor mortis*, and also the relation between the course of *rigor mortis* as affected by these variables, the formation of lactic acid in the muscle, and the degradation of certain acid-soluble, phosphorus-containing fractions of the muscle. A previous investigation had indicated that the major early *post mortem* changes in phosphorus-containing compounds of sterile fish muscle was confined to the group of compounds that are soluble in acid (Tomlinson *et al.*, 1960). In addition, this group is known to include compounds (e.g. nucleotides, phosphorylated sugars, phosphocreatine) (Tarr, 1949) that are intimately related in warm-blooded animals and probably also in fish (Tarr, 1958; Gumbmann *et al.*, 1958; also *vide supra*) to muscular function and to *rigor mortis*.

METHODS AND MATERIALS

FISH

Kamloops trout (*Salmo gairdneri*) were obtained from the Cultus Lake, B.C., hatchery of the British Columbia Provincial Fish and Game Department. Starry flounders (*Platichthys stellatus*) were captured by beach seine in the Coal Harbour area of Burrard Inlet, B.C. The trout and flounders were held live in the Vancouver Public Aquarium until required. Sockeye salmon (*Oncorhynchus nerka*) were caught by gill net in the mouth of the Fraser River, B.C., and by purse seine at Point Roberts, Washington, U.S.A., under commercial fishing conditions.

TREATMENT OF FISH PRIOR TO KILLING AND METHOD OF *Post-mortem* STORAGE

Trout and flounders were treated in one of three ways prior to killing. One group was captured (hand net) and killed by a blow on the head as quickly as possible. These fish are termed "unexercised" (Black, 1955). A second group was forced to swim vigorously for 30 minutes before being killed. These are termed "exercised". A third group was given the same treatment as the second group, followed by a period of struggling in air (10 minutes for trout, 20 minutes for flounders) before being killed. These are termed "exhausted". It was thought that the condition of the exhausted fish would probably correspond to that of most commercially caught fish on the Pacific coast. The flounders were difficult to exercise. They did not maintain a steady swimming rate as did the trout and for periods of time refused to swim at all. When left in air they struggled only spasmodically when disturbed.

Sockeye salmon were caught under commercial conditions, but records were kept of the condition of the fish on landing (e.g. lively, exhausted, dead) and of their subsequent treatment. Some were killed immediately after landing by a blow on the head, while others were allowed to die in air under the usual commercial conditions.

The circumstances under which all the fish died are recorded in the Tables.

Post mortem, pairs of fish as nearly alike as possible as to size and treatment immediately before killing were stored in the round, one of each pair in ice, the other at the prevailing temperature of the room or boat. These temperatures were recorded. The method of storage is indicated in the Tables. These two methods of storage are commonly used on this coast for fish that are later canned or frozen.

SAMPLING

All samples from trout and sockeye salmon were taken from the lateral-dorsal muscle, while those from flounders were taken from the muscle of the under side of the fish. Samples were frozen in liquid nitrogen immediately after being removed, placed in polyethylene bags, and stored at -30°C until they could be analysed. Each sample weighed 5 g or more. Samples were taken immediately

after the fish died and again after suitable intervals of storage. These intervals were so chosen that, as nearly as possible, samples representative of the onset of rigor, full rigor, softening, and complete resolution of rigor, were obtained.

OBSERVATION OF *Rigor mortis*

Onset and duration of *rigor mortis* were observed by holding the fish by the head and noting the rigidity of the body (Cutting, 1939) and also by feeling the firmness and elasticity of the flesh.

CHEMICAL METHODS

Frozen samples (5 g) were weighed and, while still frozen, were homogenized in a Servall Omni-Mixer with 30 ml of 11.4% (w/v) ice-cold trichloroacetic acid (TCA). The homogenate was centrifuged at 18,000 *g* for 15 minutes at 0°C. The supernatant solution was decanted and stored at 0°C, then the residue was re-extracted twice with 30 ml of 10% (w/v) ice-cold TCA. These two extracts were combined with the first, and the residue was discarded.

Phosphorus fractions were determined, in duplicate, on the extracts as described below. All measurements of phosphorus were made by the method of King (1932):

(a) *Inorganic phosphorus* (I-P)

This was precipitated from an aliquot of the freshly prepared extract by the method of Mathison (1909); the precipitate was washed with ice-cold 2% ammonia solution and then dissolved in 5% TCA solution for estimation.

(b) *Molybdate-labile phosphorus* (ML-P)

This fraction, together with I-P, was determined on a second aliquot of the freshly prepared extract by the method previously described (Tomlinson *et al.*, 1960). The difference between the phosphorus determined in this manner and that found in (a) above constitutes the ML-P. The phosphorus of this fraction is probably derived chiefly from phosphocreatine (Ennor and Rosenberg, 1952) but the phosphorus of certain other compounds would also appear here (e.g. ribose-1-phosphate and acetyl phosphate) (Lowry and Lopez, 1946) and in addition a small percentage of the phosphorus of several other compounds (e.g. adenosine triphosphate) would be determined (Weil-Malherbe and Green, 1951).

(c) *Readily acid-hydrolyzable phosphorus* (AL-P)

This was determined by the method of LePage and Umbreit (1948). This fraction is derived principally from adenosinetriphosphate (Bailey, 1949), but phosphorus from other compounds (e.g. adenosinediphosphate, hexose diphosphate, glucose-1-phosphate) would also appear here.

(d) *Acid-stable phosphorus* (AS-P) and *total acid-soluble phosphorus* (T-P)

The AS-P is the difference between the T-P of the extract determined by the method of King (1932), and the combined phosphorus of fractions (a), (b), and (c) above. This fraction includes the phosphorus of adenylic acid, inosinic acid, the AS-P of adenosine di- and triphosphate, the phosphorus of various phosphorylated sugars and possibly other compounds. Lactic acid was determined by the method of Barker and Summerson (1941).

In Table I analytical data are presented indicating the degree of agreement between different samples from the same fish and between samples from different fish. These fish were killed in an unexercised condition and at once frozen in liquid nitrogen. The data for ML-P suggest that the flounder and one trout (fish b, Table I) were perhaps not as unexercised as they were thought to be.

TABLE I. The acid-soluble phosphorus and lactic acid content of the muscle of freshly killed fish.²

Species	Milligrams phosphorus per gram of muscle					Lactic acid
	I-P	ML-P	AL-P	AS-P	T-P	
Rainbow trout						mg/g muscle
(a) Average ³	0.82	0.46	0.47	0.52	2.27	2.38
Range	0.80-0.84	0.44-0.47	0.43-0.49	0.50-0.53	2.24-2.29	2.29-2.48
(b) Average ³	1.36	0.05*	0.43	0.57	2.41	0.78
Range	1.31-1.45	0-0.11	0.40-0.46	0.51-0.63	2.30-2.52	0.71-0.93
Starry flounder						
Average ⁴	1.32	0.04	0.19	0.43	1.98	0.49
Range	1.25-1.46	0.01-0.07	0.15-0.22	0.37-0.47	1.85-2.19	0.43-0.59

²All fish were unexercised. The starry flounder had been in captivity about 2 months.

³Of four samples of lateral-dorsal muscle—fish (a) weighed 260 g, fish (b) 120 g.

⁴Of six samples of white muscle from the underside of the fish—fish weighed 320 g.

As will be seen in other results tabulated later, some variation between individual fish, previously paired to be as nearly alike as possible as to size and treatment before killing, is a difficulty we have been unable to overcome. A second limitation of the work is indicated by the data for ML-P for trout b and the flounder. Owing to the relatively large quantity of inorganic phosphorus present in the extracts, the error of the method of measurement of phosphorus introduces a variation of about ± 0.025 mg P/g of muscle into the estimation of each fraction. For this reason, beyond the fact that the quantity is very small, little meaning can be attached to any fraction if the quantity of phosphorus it contains is less than about 0.1 mg/g of flesh.

RESULTS AND DISCUSSION

Tables II and III record the results of an experiment with rainbow trout and starry flounders. To provide a clearer presentation of certain events accompanying the onset of rigor observed in this experiment and to confirm the very marked difference in the relation found between lactic acid production and rigor at 20 and 0°C, an experiment with unexercised trout was performed in which samples were taken at shorter time intervals. The results are shown in Table IV.

In general, the effects of the degree of exhaustion of the fish at death and of the storage temperature *post mortem* on the time-course of rigor, are in agreement with those previously described by others. That is, the greater the degree of exhaustion of the fish at death and the higher the storage temperature, the earlier

TABLE II. *Rigor mortis*, acid-soluble phosphorus and lactic acid in the muscle of rainbow trout as influenced by the degree of exhaustion of the fish at death and of the subsequent storage temperature. Weight of fish about 300 g each.

Time <i>post mortem</i> <i>hours</i>	Condition of fish	mg P per gram of muscle					Lactic acid <i>mg/g muscle</i>
		I-P	ML-P	AL-P	AS-P	T-P	
<i>Stored without ice, air temperature 17 to 19°C</i>							
0	(1) Unexercised	0.84	0.51	0.59	0.55	2.50	1.22
1	Limp	1.38	0.17	0.44	0.45	2.44	3.48
3.5	Very slight stiffening	1.27	0.26	0.60	0.38	2.51	4.82
8.5	Nearly full rigor	1.64	0.09	0.35	0.43	2.51	5.31
13.5	Full rigor	—	—	—	—	—	—
24	Softening	2.14	0.00	0.14	0.23	2.51	6.64
34.5	Soft	2.00	0.06	0.13	0.19	2.37	6.77
0	(2) Exercised	0.75	0.37	0.63	0.64	2.39	1.97
1	Limp	1.09	0.32	0.51	0.47	2.39	2.34
3.5	Very slight stiffness	1.34	0.13	0.48	0.49	2.43	3.72
8.5	Full rigor	1.88	0.12	0.06	0.30	2.36	5.64
13.5	Softening	—	—	—	—	—	—
24	Soft	1.84	0.13	0.01	0.23	2.21	5.09
34.5	Soft	1.89	0.08	0.01	0.19	2.17	5.62
0	(3) Exhausted	1.38	0.18	0.31	0.37	2.23	4.44
1	Full rigor	1.97	0.23	0.04	0.33	2.36	4.99
3.5	Full rigor	1.90	0.11	0.00	0.30	2.28	5.53
8.5	Soft	1.87	0.13	0.01	0.27	2.28	5.63
24	Soft	1.94	0.04	0.06	0.15	2.19	4.86
34.5	Soft	1.79	0.11	0.05	0.15	2.09	5.19
<i>Stored in ice</i>							
0	(4) Unexercised	1.06	0.22	0.61	0.51	2.40	1.48
1	Limp	1.08	0.17	0.47	0.54	2.26	1.61
3.5	Limp	1.01	0.29	0.56	0.49	2.35	1.67
8.5	Limp	1.19	0.15	0.34	0.43	2.11	2.28
14.5	Fairly stiff	1.65	0.07	0.24	0.42	2.38	3.05
23.5	Full rigor	1.61	0.12	0.07	0.36	2.16	3.59
48.5	Full rigor	1.67	0.08	0.11	0.33	2.19	4.59
58.5	Full rigor	—	—	—	—	—	—
79.5	Softening	1.46	0.12	0.08	0.30	1.95	4.17
0	(5) Exercised	1.25	0.03	0.49	0.37	2.14	3.21
1	Limp	1.39	0.05	0.37	0.42	2.23	2.74
3.5	Limp	1.37	0.07	0.28	0.40	2.12	3.42
8.5	Full rigor	1.62	0.10	0.04	0.42	2.18	4.13
14.5	Full rigor	1.79	0.03	0.01	0.43	2.25	4.50
23.5	Full rigor	1.76	0.06	0.04	0.40	2.25	4.50
48.5	Full rigor	1.62	0.09	0.05	0.30	2.01	4.89
58.5	Soft	—	—	—	—	—	—
79.5	Soft	1.57	0.00	0.00	0.26	1.83	4.07
0	(6) Exhausted	1.79	0.22	0.14	0.43	2.45	4.84
1	Full rigor	2.04	0.04	0.01	0.38	2.46	4.20
3.5	Full rigor	1.82	0.01	0.05	0.38	2.26	5.30
8.5	Full rigor	1.93	0.00	0.01	0.39	2.32	4.49
14.5	Softening	1.96	0.07	0.04	0.40	2.47	3.83
24	Soft	1.90	0.00	0.04	0.33	2.27	3.95
49	Soft	1.80	0.06	0.04	0.32	2.21	4.12
79	Soft	1.87	0.00	0.00	0.27	2.15	4.29

TABLE III. *Rigor mortis*, acid-soluble phosphorus and lactic acid in the muscle of starry flounder as influenced by the degree of exhaustion of the fish at death and of the subsequent storage temperature. Weight of fish about 300 g each.

Time <i>post mortem</i> <i>hours</i>	Condition of fish	mg P per gram of muscle					Lactic acid <i>mg/g muscle</i>
		I-P	ML-P	AL-P	AS-P	T-P	
<i>Stored without ice, air temperature 17 to 19°C</i>							
0	(1) Unexercised	1.11	0.17	0.23	0.37	1.87	1.08
1	Limp	1.05	0.10	0.30	0.32	1.77	1.28
3.5	Very slight stiffening	1.17	0.03	0.37	0.35	1.92	2.19
8.5	Nearly full rigor	1.35	0.11	0.18	0.27	1.91	3.25
14.5	Full rigor	1.56	0.15	0.01	0.30	2.02	3.44
24	Softening	1.61	0.09	0.04	0.20	1.95	2.55
33.5	Soft	1.62	0.04	0.06	0.19	1.92	3.44
0	(2) Exercised	1.10	0.07	0.36	0.25	1.77	0.86
1	Limp	1.38	0.10	0.35	0.29	2.12	1.08
3.5	Very slight stiffening	1.11	0.00	0.34	0.25	1.69	1.82
8.5	Full rigor	1.33	0.07	0.17	0.16	1.74	2.34
14.5	Full rigor	—	—	—	—	—	—
24.5	Soft	1.45	0.12	0.08	0.08	1.72	2.38
33.5	Soft	1.39	0.09	0.05	0.06	1.58	1.57
0	(3) Exhausted	1.20	0.07	0.20	0.24	1.71	2.15
1	Slight stiffening	1.12	0.12	0.25	0.17	1.66	1.78
3.5	Full rigor	1.33	0.10	0.14	0.21	1.79	2.67
8.5	Full rigor	1.40	0.15	0.04	0.12	1.72	3.18
14.5	Full rigor	—	—	—	—	—	—
24	Softening	1.35	0.09	0.07	0.13	1.67	2.68
33.5	Soft	1.56	0.02	0.00	0.04	1.61	2.32
<i>Stored in ice</i>							
0	(4) Unexercised	0.97	0.24	0.15	0.30	1.66	0.37
1	Limp	0.85	0.20	0.25	0.23	1.53	0.56
3.5	Limp	0.97	0.17	0.23	0.25	1.63	0.84
8.5	Limp	0.99	0.14	0.27	0.29	1.69	1.06
14.5	Slight stiffening	0.99	0.18	0.12	0.28	1.57	1.89
24	Full rigor	1.19	0.08	0.06	0.25	1.57	1.63
48	Full rigor	1.10	0.14	0.07	0.14	1.44	2.33
79	Softening	0.97	0.16	0.07	0.09	1.29	1.92
0	(5) Exercised	0.93	0.18	0.09	0.22	1.58	0.93
1	Limp	0.91	0.14	0.08	0.24	1.92	0.91
3.5	Stiffening	1.07	0.07	0.04	0.19	1.55	1.07
8.5	Full rigor	1.16	0.07	0.00	0.13	1.91	1.16
24	Softening slightly	1.07	0.09	0.00	0.14	1.48	1.07
48	Softening	0.62	0.08	0.02	0.07	1.30	0.62
80	Soft	0.63	0.13	0.08	0.07	1.12	0.63
0	(6) Exhausted	1.09	0.10	0.22	0.30	1.77	2.26
1	Limp	1.09	0.06	0.20	0.33	1.69	1.95
3.5	Stiffening	1.09	0.17	0.11	0.31	1.76	2.74
8.5	Full rigor	1.13	0.07	0.05	0.30	1.74	2.62
24	Full rigor	1.12	0.10	0.03	0.26	1.69	2.78
48	Soft	1.11	0.09	0.04	0.14	1.45	2.73
84	Soft	1.12	0.08	0.05	0.07	1.32	2.24

TABLE IV. The relation between onset of *rigor mortis* and changes in the molybdate-labile phosphorus, acid-labile phosphorus and lactic acid concentration in the muscle of unexercised rainbow trout stored at 0° and 20°C. Weight of fish about 300 g each.

Time <i>post mortem</i> <i>hours</i>	Condition of fish	mg P/g of muscle		Lactic acid <i>mg/g muscle</i>
		ML-P	AL-P	
<i>Stored at 20°C</i>				
0	Limp	0.27	0.45	1.17
1	Limp	0.38	0.49	1.79
2	Limp	0.48	0.44	1.82
3	Slight stiffness	0.37	0.50	3.29
6	Near full rigor	0.06	0.22	6.64
9	Full rigor	0.14	0	7.11
12	Full rigor	0.14	0.12	7.15
15	Softening slightly	0.12	0.10	7.12
18	Softening	0.14	0	7.34
21	Softening	0.11	0.10	7.05
<i>Stored in ice</i>				
0	Limp	0.17	0.56	1.30
1	Limp	0.24	0.50	1.56
2	Limp	0.34	0.53	1.45
3	Limp	0.42	0.48	1.49
6	Limp	0.19	0.43	1.99
9	Slight stiffness	0.08	0.25	2.34
12	Increased stiffness	0	0.23	2.68
15	Near full rigor	0.06	0.14	2.30
18	Full rigor	0	0.09	2.84
21	Full rigor	0.07	0.14	3.38

rigor sets in and the shorter time it persists (Ewart, 1887; Anderson, 1909; Leim *et al.*, 1927; Benson, 1928; Schlie, 1934; Cutting, 1939; Jul, 1952; Pavlov, 1956). In one apparent exception to this (the onset of rigor at the same time in the two exercised flounders (Table III)) the analytical data indicate that in fact the fish stored in ice was more nearly exhausted than exercised, presumably the result of low glycogen reserves in the muscle at the start of the exercise period.

In only five fish (Tables II and IV) was ML-P found in excess of 0.25 mg/g of muscle. These were all trout. Four were unexercised and one exercised. In each of the unexercised fish there was evidence of an increase in ML-P during a short period of time after killing. This increase occurred either directly to a higher value than that found in the freshly killed fish (two fish), or to a higher value than that reached after an initial decrease (two fish). It appears likely that the difference observed between these two pairs resulted from differences in the speed with which the initial sample was taken and that the usual course of events in the unexercised trout consists of a decrease in ML-P followed by a period of recovery. In each of these fish the ML-P decreased to very low values

soon after the recovery period. In the exercised fish the quantity decreased but only very slightly in the first hour *post mortem*. In all of the other fish that contained any appreciable quantity initially the concentration of ML-P decreased from the time of killing. In all of the fish, regardless of the initial course of events, the concentration of ML-P reached very low values while fairly high concentrations of AL-P remained in the muscle and before *rigor mortis* was fully established. With the exception of the initial changes observed in the unexercised fish, the relation between the ML-P concentration and rigor in trout and flounder is qualitatively like that observed by Fujimaki and Kojo (1953) in frigate mackerel and by Bendall (1951) in rabbit muscle. It should be pointed out that Fujimaki and Kojo examined their fish only at killing and again 4 and 8 hours *post mortem*. The quantity of ML-P found in a number of fish in the present work at the time they were killed was very low. The reason for this is not clear, but Tarr (1949) found similar low values in freshly killed fish, and suggested that they probably resulted from very rapid breakdown of phosphocreatine during struggling (see also Bendall, 1951). As will be seen below, in none of the commercially caught sockeye salmon that we have examined has any appreciable quantity of phosphorus been found in this fraction. These fish had all undoubtedly struggled vigorously before being landed.

In two unexercised trout (Table II) a marked decrease in AL-P was observed between killing and 1 hour *post mortem*, followed by an increase to about the same concentration as that found in the muscle at the time of killing. In the two unexercised flounders (Table III) there appeared to be a small increase in the phosphorus of this fraction during the first few hours *post mortem*. In each of these four fish, after these initial changes, the AL-P decreased to very low values. In the remainder of the fish, the acid-labile phosphorus either decreased from the time of killing, or after a short initial period during which it remained fairly constant.

In all of the fish, it is clear that the onset and development of rigor occurred during the period of time when the concentration of AL-P in the muscle was decreasing to a very low value. Full rigor did not appear to become established until the phosphorus of this fraction had nearly disappeared. This is in agreement with the previous findings of Noguchi and Yamamoto (1955a, b) who studied the *post-mortem* changes in the contractability of fish muscle (in response to perfusion with water) in relation to the amount of AL-P the muscle contained.

It is interesting that the range of concentration of AL-P over which rigor became established in the fish is similar to that (about 0.4 mg/g and lower) over which it became established in rabbit psoas muscle (Bate-Smith and Bendall, 1947; Bendall, 1951) and in whale muscle (Marsh, 1952). There was a tendency for the onset of rigor to occur at higher concentrations of AL-P in fish muscle at 20°C than at 0°C. It appears from this that a similar relation between the

critical level of adenosinetriphosphate (for onset of rigor), temperature, and pH may exist for fish as was found for rabbit muscle by Bendall (1951). However, the present data are insufficient to establish this.

The phosphorus of the acid-stable fraction decreased *post mortem*, but unlike that of the molybdate-labile and acid-labile fractions, did not fall rapidly to low values during the onset of rigor, but rather continued to decrease at a fairly steady rate during rigor. By the time rigor was resolved, the phosphorus of this fraction in trout had decreased to a value of about 0.3 mg/g of muscle or less, while in flounder it was generally down to 0.2 mg/g or less.

In unexercised fish (Tables II to IV) it will be seen that there was a different relation between the course of formation of lactic acid and the onset of rigor at 0°C and at room temperature. At the higher temperature, the concentration of lactic acid in the muscle reached its maximum value at about the time full rigor was established, whereas at 0°C full rigor was established while lactic acid was still being actively formed and had reached only about 50% of its final maximum concentration. In exhausted fish, on the other hand, at either temperature the maximum concentration of lactic acid was reached either by the time full rigor was established or very soon thereafter. In exercised fish, as would be expected, the course of events tended to be intermediate between these two extremes.

Although it has long been known that the occurrence of rigor is not dependent on lactic acid formation (Hoet and Marks, 1926) the available data indicate that there is a relation between the duration of rigor in fish and the quantity of lactic acid accumulated in the muscle *post mortem*. That is to say, the greater the concentration of lactic acid reached (or the lower the pH of the muscle) the longer would rigor endure (Reay and Shewan, 1949). In the present work, while there is some evidence for such a relation in the fish stored at room temperature, a different relation is evident in those stored in ice. In these fish it appears that the longer lactic acid continues to be produced *post mortem*, the longer is the time before rigor is resolved. This relation can also be seen in the data for the fish stored at room temperature. A portion, but by no means all, of the increase in time results from delay in onset. Although, as previously thought, the establishment of a low pH in fish muscle may be a factor in prolonging the duration of rigor, it does not seem to be unreasonable to suggest that for rigor to persist once it has been established, it may also be necessary that an energy-yielding process be proceeding in the muscle and that once this process has ceased, or decreased to a very low rate, then rigor begins to disappear. It is interesting to recall Ewart's remark made in 1887: "If before the rigor appears the latent energy of the muscles has all but exhausted . . . the rigor though well marked will be of short duration, while on the other hand, if a considerable amount of rigor producing material [unspecified] is left when the stiffening supervenes, the rigor, though not strikingly resembling a tetanic spasm will be more intense and more persistent."

A number of sockeye salmon were caught under commercial conditions and examined in the same fashion as were the trout and flounders. The data obtained (Tables V to VII) are quite similar to those recorded above for exercised or

TABLE V. *Rigor mortis*, acid-soluble phosphorus and lactic acid in the muscle of gill-net caught sockeye salmon as affected by the condition of the fish at killing and the storage temperature.⁵

Time <i>post</i> <i>mortem</i>	Condition of fish	mg P per gram of muscle				Lactic acid	Time to	
		I-P	ML-P	AL-P	AS-P		Onset of rigor	End of full rigor
<i>hours</i>						<i>mg/g muscle</i>	<i>hours</i>	<i>hours</i>
<i>Stored without ice⁶</i>								
0	(1) Lively, killed on landing	1.37	0.00	0.34	0.38	5.94	1	6
4	Full rigor	1.89	0.04	0.04	0.25	8.53		
16	Soft	1.95	0.00	0.00	0.11	8.77		
0	(2) Exhausted, killed on landing	1.49	0.07	0.28	0.46	5.90	1	5
3	Full rigor	1.82	0.06	0.06	0.38	7.32		
16	Soft	1.83	0.17	0.03	0.13	7.84		
0	(3) Allowed to die in air	1.22	0.18	0.30	0.59	6.14	1	3
3	Full rigor	1.66	0.15	0.09	0.34	9.24		
16	Soft	1.70	0.19	0.06	0.35	8.31		
0	(4) Dead on landing	1.27	0.06	0.28	0.50	6.12	<1	4
3	Full rigor	1.53	0.15	0.02	0.41	8.64		
17	Soft	1.59	0.04	0.07	0.33	8.65		
<i>Stored in ice</i>								
0	(5) Like (1)	1.07	0.09	0.57	0.41	—	4	17
1	Limp	1.05	0.12	0.53	0.36	4.05		
4	Limp	1.36	0.04	0.37	0.39	6.05		
13	Full rigor	1.51	0.10	0.00	0.36	7.97		
45	Softening	1.52	0.19	0.00	0.34	8.25		
72	Soft	1.52	0.00	0.00	0.24	5.53		
0	(6) Like (2)	1.15	0.04	0.36	0.49	5.61	1	17
1	Limp	1.30	0.00	0.19	0.40	6.70		
3	Full rigor	1.34	0.00	0.09	0.33	6.44		
13	Full rigor	1.46	0.05	0.04	0.34	7.96		
45	Softening	1.67	0.00	0.00	0.38	8.74		
72	Soft	1.57	0.00	0.00	0.36	8.38		
0	(7) Like (3)	1.36	0.09	0.28	0.43	5.76	<1	15
3	Full rigor	1.57	0.07	0.02	0.50	7.57		
23	Softening	1.66	0.00	0.04	0.41	7.84		
48	Soft	1.71	0.00	0.03	0.36	6.41		
0	(8) Like (4)	1.31	0.00	0.41	0.36	4.76	1	15
3	Full rigor	1.58	0.03	0.00	0.44	6.56		
23	Softening	1.62	0.01	0.00	0.37	7.49		
48	Soft	1.47	0.08	0.07	0.35	6.96		

⁵These fish weighed about 6 lbs each and were caught in the mouth of the Fraser River near Steveston, B.C., July 26–27, 1960. The water temperature was 18°C.

⁶The storage temperature for the fish stored without ice was 24°C at the start and decreased to about 20°C at the end of the experiment.

TABLE VI. Acid-soluble phosphorus and lactic acid in the muscle at the time of landing and the course of *rigor mortis* in sockeye salmon from a single gill net set.⁷

Appearance of fish at landing	mg P per gram of muscle				Lactic acid <i>mg/g muscle</i>	Time to	
	I-P	ML-P	AL-P	AS-P		Onset of rigor <i>hours</i>	End of full rigor <i>hours</i>
Fairly lively	1.02	0.0	0.62	0.49	5.87	1	5
" "	0.97	0.14	0.54	0.49	5.42	1	5
Exhausted	1.09	0.10	0.43	0.55	5.95	1	3
"	1.04	0.17	0.35	0.54	6.26	1	3
"	1.09	0.17	0.32	0.55	6.09	1	5
"	0.99	0.12	0.35	0.60	5.46	1	4
"	1.11	0.19	0.43	0.61	5.96	1	4
Dead	1.16	0.17	0.30	0.48	6.26	<1	4

⁷These fish, each weighing about 6 lb, were taken from the Fraser River near Albion, B.C., July 31, 1960. The fish were swimming upstream against a strong current. They were selected from various points along the length of the net and were killed by a blow on the head and at once sampled as they were landed. The set lasted 30 minutes. For observation of *rigor mortis* they were stored without ice at a temperature of 19°C.

All fish were judged to be completely out of rigor 14 hours *post mortem*.

exhausted trout. A somewhat higher maximum concentration of lactic acid was found to accumulate in the salmon than in the trout. The very marked influence of icing in prolonging the duration of rigor is obvious and as in the trout appears to be related to a reduction in the rate of glycolysis. It is also evident that even in these commercially caught fish there is a large production of lactic acid *post mortem*. The salmon weighed about 6 pounds each compared to about $\frac{1}{2}$ pound for trout and would therefore be expected to cool more slowly in ice; consequently, it is likely that a more efficient system of chilling could lengthen the duration of rigor in salmon.

Under conditions of elevated summer temperatures it is clear that if processing cannot be carried out within a very short time of catching, icing would be most beneficial. It should be pointed out that to derive the greatest benefit from icing it must be carried out as quickly as possible after the fish are landed in order to take the fullest advantage of the energy reserves of the muscle. The data for the salmon (particularly Table VI) indicate that at landing they are remarkably uniform but such differences as are seen, and also the noticeable effect of allowing the fish to die in air after landing, rather than killing them at once, suggest that important increases in duration of rigor in salmon could be effected if a method of catching were used that would greatly shorten the period from first contact to killing. Although, as suggested by Reay and Shewan (1949), this possibility may be only of academic interest now, it exists and should not be overlooked.

TABLE VII. *Rigor mortis*, acid-soluble phosphorus and lactic acid in seine-caught sockeye salmon as affected by the condition of the fish at killing and the storage temperature.⁸

Time <i>post mortem</i> <i>hours</i>	Condition of fish	Mg P per gram of muscle				Lactic acid <i>mg/g muscle</i>	Time to	
		I-P	ML-P	AL-P	AS-P		Onset of rigor <i>hours</i>	End of full rigor <i>hours</i>
<i>Stored without ice⁹</i>								
0	(1) Killed on landing	1.18	0.17	0.34	0.53	5.57	1	3*
3	Full rigor	1.40	0.11	0.0	0.43	8.73		
19	Soft	1.83	0.0	0.0	0.26	9.96		
0	(2) Killed 4 minutes after landing	1.23	0.11	0.48	0.42	5.96	1	2*
3	Full rigor	1.76	0.08	0.02	0.40	9.82		
19	Soft	1.70	0.11	0.06	0.33	9.86		
0	(3) Died in air, 15 minutes after landing	1.45	0.05	0.20	0.43	6.55	<1	1*
3	Full rigor	1.70	0.0	0.03	0.35	9.95		
19	Soft	1.86	0.0	0.07	0.35	9.76		
<i>Stored in ice</i>								
0	(4) Like (1)	0.96	0.19	0.50	0.47	4.95	3	16**
3	Stiffening	1.19	0.06	0.38	0.46	4.46		
6	Full rigor	1.55	0.01	0.06	0.55	5.81		
19	Full rigor	1.74	0.0	0.01	0.49	6.57		
43	Softening— firmer than (5) and (6)	1.86	0.0	0.06	0.40	7.14		
0	(5) Like (2)	1.19	0.11	0.46	0.53	5.16	1	18**
2.5	Near full rigor	1.23	0.18	0.18	0.46	6.27		
6	Full rigor	1.31	0.13	0.04	0.48	6.36		
19	Full rigor	1.61	0.16	0.03	0.48	7.35		
43	Softening	1.69	0.15	0.0	0.49	7.28		
0	(6) Like (3)	0.90	0.18	0.50	0.50	5.66	<1	18**
2	Near full rigor	1.38	0.07	0.25	0.36	5.59		
6	Full rigor	1.47	0.08	0.06	0.44	7.02		
19	Full rigor	1.64	0.0	0.08	0.39	7.74		
43	Softening	2.10	0.08	0.05	0.32	8.10		

⁸These fish were caught at sea near Pt. Roberts, Washington, U.S.A., Aug. 10, 1960.⁹Air temperature increased from 25°C to 28°C in 3 hours *post mortem*, then decreased to 23°C at 19 hours.*These fish were all judged to be completely out of rigor 6 hours *post mortem*, with the order of firmness at that time being 1>3>2.**Unfortunately observations of these three fish were not made between 19 and 43 hours *post mortem*, consequently the duration of full rigor is not known and the times given are minimum values.

ACKNOWLEDGMENTS

The authors wish to express their thanks to Dr Murray A. Newman, Curator, Vancouver Public Aquarium Association, for his very helpful advice and for the use of Aquarium facilities, and to Mr Loyd A. Royal, Director of Investigations, International Pacific Salmon Fisheries Commission, and Mr S. B. Smith, Divisional Fishery Biologist, British Columbia Department of Recreation and Conservation, Fish and Game Branch, for many of the fish used in this work.

Note added in proof

Since this paper was submitted for publication, a further paper by N. R. Jones and J. Murray has appeared (*Zeitschrift für vergleichende Physiologie*, 44: 174-183 (1961)) in which they have described the relation between *rigor mortis* and changes in the concentrations of nucleotides in codling (*Gadus callarias*) muscle at 0°C.

In contrast to our findings with unexercised trout and flounders, in which the concentration of acid-labile P was maintained for several hours *post mortem* at 0°C, Jones and Murray found that there was no observable maintenance of the adenosinetriphosphate level in codling muscle under the same conditions. This difference may have arisen as a result of species differences or of nutritional differences between the fish used in the two investigations. Jones and Murray compared their results with the known maintenance of adenosinetriphosphate for a period of time *post mortem* in mammalian muscle, and suggested the difference resulted from the very low concentration of glycogen in fish muscle. Our results indicate that at least in certain fish the difference between mammalian and fish muscle is not so great as to preclude the maintenance of adenosinetriphosphate for some time *post mortem* in the latter.

A point of interest that arises from a consideration of the results recorded in these and other papers is the fact that pre-rigor fish even of the same species are not necessarily uniform biochemically and can have quite different concentrations of acid-soluble phosphorus compounds and lactic acid in their muscles depending on their previous history. This fact should be taken into account in investigations dealing with pre-rigor freezing of fish.

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Variability in Aerial Counts of Spawning Salmon^{1,2}

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ABSTRACT

A study of spawning ground surveys for pink salmon (*Oncorhynchus gorbuscha*) was made in two streams on Kodiak Island. An experimental design is described which permits replication of observers' counts of spawning salmon. The variance in an observer's estimate was found to be proportionate to the size of the estimate. The experiments indicated that an observer will detect differences in population size of plus or minus 50%. The relationship between counts of one observer and another changes within different streams, but within each river the observations of one observer were correlated with those of another. The results of the experiments are summarized in recommendations for aerial surveys of spawning salmon.

INTRODUCTION

EACH SUMMER in Alaska salmon return to spawn and die in their native streams. The abundance of spawners in the streams and the number taken by fishermen affect the health of the runs. Counts of abundance of spawners are therefore important to both industry and regulatory agencies. During fishing seasons the fishery is often opened or closed depending on current estimate of the size of escapement.

Runs to some of the more important streams are counted through weir fences or past observation towers. This is the case for the sockeye or red salmon (*Oncorhynchus nerka*) of Bristol Bay. There the bulk of the run enters into half a dozen rivers where the salmon may be enumerated in the trunk stream before dispersal to many tributaries.

The situation is different with two other species, the pink and chum salmon (*O. gorbuscha* and *O. keta*), in other parts of Alaska. Pinks and chums spawn in about 2000 rivers, large and small, spread over an extended coastline. The variability is great between streams and the number of streams that must be enumerated is large. It is not economically feasible to make direct counts with weirs or towers in every stream. The abundance of spawners in several hundred streams is estimated by visual observations from airplanes.

It is obvious that direct counts cannot be made of every fish in a stream while the observer flies overhead at 70 to 100 miles an hour. Spawning populations often number up to several hundred thousand and may occupy only a few miles of river with several spawners to a square yard. We must rely on an estimate of some sort. The method commonly used is to count by hundreds

¹Received for publication October 7, 1959.

²Contribution No. 61, College of Fisheries, University of Washington.

or by thousands. The number of fish required to fill the counting unit of 100 or 1000 must be estimated. The number of these estimates multiplied by the basic counting unit supplies the total count. This paper is concerned with measuring the variability of this type of estimation.

The problems of measuring the accuracy or precision of escapement enumeration have received little attention in fisheries literature. Atkinson (1944) was one of the first to consider the problem. He recognized that the spawners were not a stationary population and that new entrants arrived to take the place of those that died after spawning. Thus any estimate made at one time will not correctly estimate the total number of spawners. With a knowledge of the length of life of the individuals and by conducting several surveys it is possible to correct for this type of error (Gangmark and Fulton, 1952).

The changing population is not the only reason why an individual count does not provide the total number of spawners. Many fish remain unobserved in deep pools, under overhanging brush or trees, or below the limits of visibility in turbid glacier-fed rivers.

Observations will give at best an index, an unknown portion, of the number of spawners, even if corrected for the changing population. In practice it is more convenient to determine the maximum rather than the average observed population. Assuming that the length of life of individuals on the spawning ground is relatively constant from year to year we can use the maximum observed abundance as an index to the number of spawners.

It is the variability in this index that will be the subject of our discussion. We will limit ourselves to the variation in the index that measures peak abundance and will not consider the differences between the index and the true population.

We are dealing with the ability of human beings to estimate numbers. Unfortunately this seems to be a field that has been neglected by psychologists. The only studies that have been made deal with the ability to perceive a small number of objects or the time period required to differentiate between groups of different numbers. These studies have little application to our problem.

We are evaluating a perceptual matter and doing so in a subjective manner. In most cases where physical quantities or properties are very complex or poorly understood we turn to a subjective method of evaluation. Measures of taste flavors or of personal comfort are examples. Advocates of subjective measurements usually argue for them on the basis of impracticability of physical measurements for the purposes intended. The difficulties usually recognized are that the evaluation will suffer variability between and within observers. Less often the difficulties in training of observers are discussed.

The subjective method will be usable if we do not require a high degree of accuracy. In fact, in surveys to be discussed each single judgment need not be correct. Hopkinson (1953) has pointed out that the mean of a convenient number of judgments should not drift and that the variance of the judgments should be small in relation to the differences in which the experiment is interested.

Thompson³ discussed spawning survey estimates based on the completely subjective ratings of *good*, *fair* or *poor*, accompanied by numerical estimates. He found that often escapements rated by one observer as poor were associated with higher numerical counts than estimates rated good by another observer. He questioned the comparability of different observers and suggested that standardized methods be applied.

The problem of estimating large numbers was considered by Rae (1952) in estimating the numbers of plankton in a microscope transect. He found that estimates were consistent, with little difference between observers.

In this paper our objectives are to determine the precision of the spawning survey indices and to determine some of the factors which affect them by replicating the observations.

* - METHODS

The study was made in two streams on Kodiak Island (at Uyak and Deadman Bays). These streams are of moderate size and have had peak spawning counts of pink salmon between 10,000 and 150,000 in the past 10 years. The physical characteristics of the streams are similar to many other salmon spawning rivers in Alaska (Fig. 1). The variability due to weather conditions and water turbidity was minimized by conducting all observations during good weather and during normal stream flows.

In order to avoid personal bias, the earlier estimates of an observer should not be allowed to prejudice his subsequent estimates of the same group of fish. This was avoided by having the observer make his counts in such a manner that he was not aware of the total he was reporting.

Each stream was divided into two sections which included the total spawning area of the stream. Counts were made of the total stream as well as each section. The counts were made by estimating groups of 100's and 1000's while flying both upstream and downstream. Thus each section and the total stream were counted four times. Prior to each flight the order in which the sections were to be counted was determined by lot, with the restriction that no section would be counted twice in a row by the same counting unit. This meant that after a particular section of stream was counted either a new section or another counting unit was presented.

For further insurance that the counts would not be remembered, the number of estimated basic units was registered on a hand counter in the following manner. The pilot recorded the section being counted, direction of flight, and a number that he set on the dials of the hand counter. He then handed the counter to the observer after sealing the dials with a piece of opaque tape. The observer recorded the number of estimates of the counting unit immediately as they were sighted by pressing the lever on the counter. When the section was completed

³Thompson, W. F. 1948. Memorandum for stream surveys for scientific personnel. Fisheries Research Institute, University of Washington; unpublished.



FIG. 1. Deadman River, Kodiak Island. Photo by Ron Lopp. Section C of the stream extends from the mouth up to the point "P". Section D extends from "P" to "Q".

the observer recorded the total appearing on the dials and reset the counter to zero before returning it to the pilot. The actual count was obtained later by subtracting the preset number from the final number recorded by the observer. This assured that neither the pilot nor observer knew the count recorded for any section.

It was not feasible to randomize the use of airplanes because of the time and expense required in landing and taking off again. Each observer completed a series of observations duplicating each section and the total of the stream and then changed airplanes.

The sections to be counted were randomized only within each stream to minimize the travel between streams. A program was completed in a stream before starting in the second stream. The same flight plan was used by each airplane and an attempt was made to make the observations at as near the same time as possible.

All counts were made from small, slow-flying airplanes. The type of airplane was similar to one commonly used for crop dusting with the exception of the addition of floats for water landings. The air speed was usually kept at about 75 miles an hour (120 km/hr). The flight altitude during observation was generally about 200 feet (33 m), but varied between 100 and 300 feet depending upon the terrain.

The variables in the experiments were observers, airplanes, methods of counting (100's or 1000's), streams, and whether counts were by total stream or by sums of sections. Three experiments were run in 1957, and another experiment was conducted over a 3-year period beginning in 1956. The estimates from each experiment are tabulated in the appendix tables.

Each observer had at least one season's experience with stream surveys and all were currently engaged in making surveys for research or management purposes at the time the experiments were undertaken.

Analysis of variance procedures were used to test hypotheses of differences between the means of the variables involved. Since the comparisons are between counts, it might seem that chi-square techniques should be used to handle enumerated observations. The counts are complicated, however, by the presence of additional variability. Although the number of fish in the stream at a particular time may follow some specified distribution, different groups of fish will have different probabilities of being counted because of variation in the ability of the observer to estimate the basic counting unit. The result of these two variations can be thought of as a measured variable rather than a precise count. Therefore, analysis of variance is applied. The original data were transformed to logarithms to correct for a proportional relationship between the means and the variances. Figure 2 shows the relationship between the means and the variances.

In applying the results of the analysis of variance we should like to consider that our primary effects are drawn randomly from a larger population. We would consider that our model of analysis was either random or possibly mixed

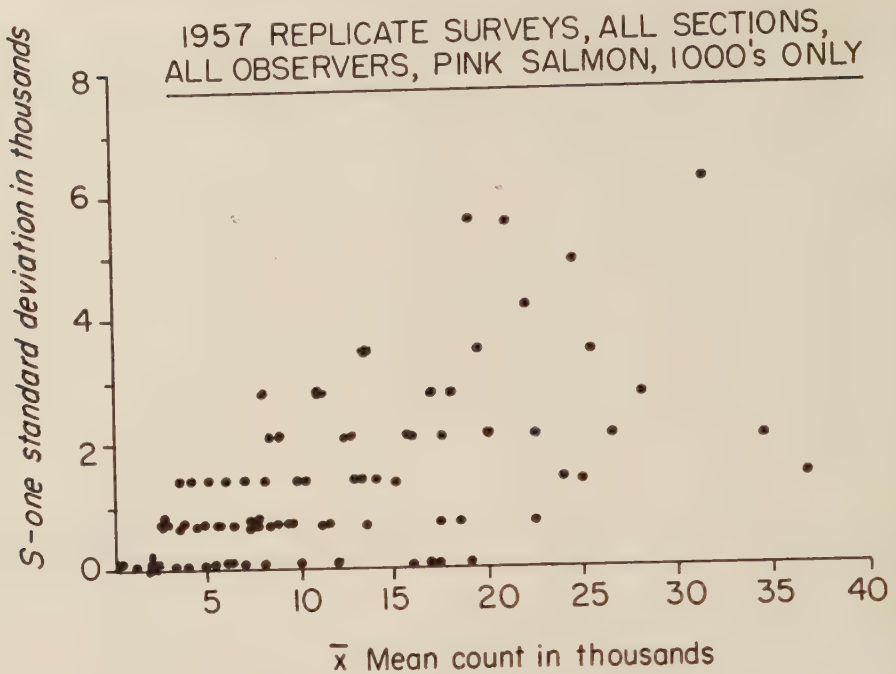


FIG. 2. Comparison of observers' mean count and standard deviation.

if we wished to consider only a particular series of streams or only two possible ways of making the counts. However, it was not feasible to obtain enough degrees of freedom for any of the main effects to have any sensitivity in a mixed model. Either we could not collect enough observers together or the time element prohibited covering a large series of streams under uniform observation conditions. Therefore we have considered a series of tests on fixed models and will make some inferences from these that may apply to other situations if the individual tests have some agreement. The difficulty is recognized of drawing conclusions about the significance of main effects when interaction is present.

RESULTS FROM THE THREE EXPERIMENTS IN 1957

The analyses of data from the 1957 experiments are summarized in Table I. A consistency in the three experiments is shown. Under main effects, significant differences were found between the means of observers and between counting methods in each of the experiments. Differences between counts from the total stream or from summing the sections were not significant in all experiments. Counts between streams were significantly different in both experiments where two streams were surveyed. In the two experiments in which more than one airplane was used there was no difference between mean counts from different airplanes.

TABLE I. Summary of analysis of variance tables—1957 experiments.
(MS = mean square; df = degrees of freedom; ** = $P < 0.01$).

Source of variation	1st experiment Observers A & C		2nd experiment Observers A, B & C		3rd experiment Observers A, D & E	
	MS	df	MS	df	MS	df
Main effects						
Observers (O)	0.0541**	1	0.0802**	2	0.1398**	2
Airplanes (A)	0.0077	1	0.0022	1	—	—
Counting methods (C)	0.3249**	1	0.1291**	1	0.4485**	1
Total counts vs section counts (T)	0.0138	1	0.00002	1	0.0091	1
Streams (S)	2.8900**	1	—	—	0.3434**	1
Interactions						
O × A	0.0563**	1	0.0023	2	—	—
O × C	0.1296**	1	0.0401**	2	0.1638**	2
O × T	0.0095	1	0.00004	2	0.0037	2
O × S	0.0049	1	—	—	0.0026	2
A × C	0.0020	1	0.0010	1	—	—
A × T	0.0005	1	0.0068	1	—	—
A × S	0.2652**	1	—	—	—	—
C × T	0.0004	1	0.0083	1	0.0002	1
C × S	0.0060	1	—	—	0.0902**	1
T × S	0.0009	1	—	—	0.0007	1
O × A × S	0.0381**	1	—	—	—	—
O × C × S	0.0027	1	—	—	0.0844**	2
Other 3-way and higher interactions	0.0036	14	0.0044	9	0.0024	7
Within	0.0020	32	0.0038	24	0.0068	24
Total		63		47		47

Results from the tests on the two-way and higher interactions were also similar in each of the three experiments. The observer-count interaction was the only interaction present in all experiments. Apparently there was a difference between observers in their ability to count by 100's or 1000's.

A three-way interaction (observer-airplane-stream) and two-way interactions (observer-airplane and airplane-stream) were present in the first experiment. These interactions were present only in the first experiment, and a check of the field notes shows that this was correlated with and probably the result of one of the observers becoming airsick in a specific airplane over one of the streams.

In the third experiment three-way observer-count-stream and two-way count-stream interactions occur. This is associated with a low numerical value for the observations in one of the streams and indicates that the ability to count by 100's or 1000's will differ depending upon the magnitude of the count. This suggests that further studies might place some limit on the numbers where estimates by 100's and 1000's may be combined.

All other two-way, three-way and higher order interactions were non-significant.

RESULTS FROM THE THREE-YEAR EXPERIMENT

Results of the analysis of variance of the experimental data from two observers over a 3-year period are shown in Table II. The main effects supply us with little additional information. Differences in observer and stream means agree with our results from the three experiments previously discussed. The difference between years, if not intuitively obvious, must be assumed to supply a justification for the existence of any survey program. Actually we know that streams vary considerably from year to year. Some even have runs only in alternative years.

TABLE II. Analysis of variance table of pink salmon replicate surveys in 1956, 1957 and 1959, on Uyak and Deadman Rivers. Observers were A and E; counts were by 1000's. (SS = sum of squares; df = degrees of freedom; MS = mean square; ** = $P < 0.01$).

Source	SS	df	MS	P
Observers (O)	0.1512	1	0.1512	**
Streams (S)	0.0398	1	0.0398	**
Years (Y)	1.0224	2	0.5112	**
Interactions				
O $\times$ S	0.2324	1	0.2324	**
O $\times$ Y	0.1010	2	0.0505	**
S $\times$ Y	0.5966	2	0.2983	**
O $\times$ S $\times$ Y	0.0241	2	0.01204	—
Within	0.1354	36	0.00376	—
Total	2,3029	47		

The main interest comes from the interactions. The presence of an observer-year interaction suggests that any difference between these two observers changes from year to year. This means that it will be difficult to determine any relationship between observers that might be used to adjust the observations to a common basis.

The observer-stream interaction indicates similar problems in trying to adjust observer differences between streams since a different factor may be necessary in different streams.

AMOUNT OF VARIABILITY

So far we have confined our discussion to the various effects that are associated with observed variations. The amount of variation is also of importance. Even though considerable variation exists, the results will be usable for purposes of an index if the variation in observation is small in comparison with changes in the abundance of fish. Actual total counts of pink salmon through weirs have shown cyclic differences as much as 800 times (5000 to 4,000,000) and

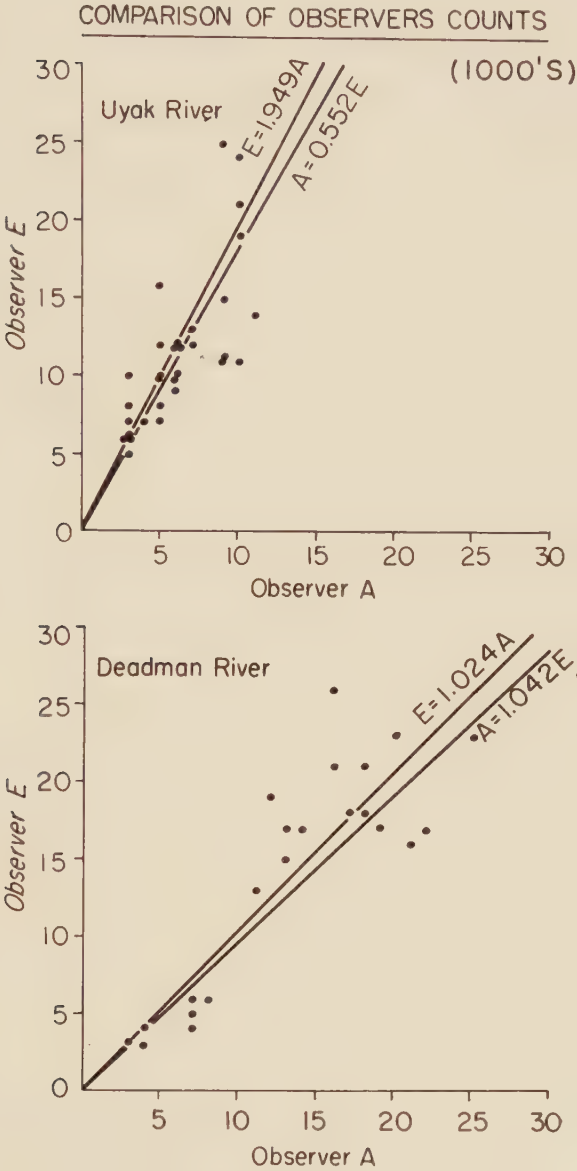


FIG. 3. Comparison of observers' counts in thousands.

variations of 10 to 15 times are very common (Rounsefell, 1958; Counts at the Snake Creek Weir⁴).

Figure 2 shows the relationship between the standard deviation computed from replicate surveys by the observers and the mean count obtained. All counts were made by 1000's and two replicates were obtained. A similar distribution was obtained by using the counts by 100's but with slightly larger standard deviations.

The limitations imposed by two replicates and the small number of observers tested should be kept in mind. The data in Fig. 2 indicate that one standard deviation of an observer's counts will not be more than $\pm 50\%$ around his mean observation. He might expect that usually it will be less than 25%. This would mean a standard deviation of 5000 for a mean count of 20,000. If we consider two standard deviations around the observer's mean we can conclude that generally speaking an observer will detect differences of $\pm 50\%$.

The magnitude of the observer-stream interaction from the 3-year experiment is shown in Fig. 3. Here the counts of the observers are paired by associating estimates made as close together as possible with respect to time. The observations by one observer are correlated with those of another in each river (Uyak, $r = 0.75$; Deadman, $r = 0.76$). However, in the case of Uyak River, there is a considerable bias between the observers, with Observer E consistently obtaining higher estimates. This is not so in Deadman River, where the regression coefficients do not differ significantly from 1.

The use of Snedecor's (1956) regression model 1A explains the fact that the coefficients of x on y and y on x are both greater than 1 for the Deadman River experiments. This model was appropriate since the variance was proportional to the counts and we assumed that the regression line passed through the origin.

RECOMMENDATIONS FOR AERIAL SURVEYS

Any use of aerial surveys should be done with a realization that the counts have value as an index and not a total count. Any calculation or compilation of survey data should be that appropriate for handling indices.

Even though stream survey counts are used only as indices, they should not be used to indicate differences of less than 50% without a careful evaluation of the variance of the observer's estimates. Only one observer should be used. If it is necessary to change observers, any factor to correct observer differences may vary from stream to stream and from year to year. Only one counting unit should be used. Substitution of different aircraft of the same type or of different experienced pilots should make little difference in the estimates obtained.

⁴Official Records of the United States Fish and Wildlife Service Snake Creek Weir, Olive Cove, Southeastern Alaska.

ACKNOWLEDGMENTS

The work reported here was supported by the salmon packers of the Kodiak Island area. I would like to acknowledge the assistance received in the field from Mr Tom Calkins of the University of Washington Fisheries Research Institute, Mr Roy Rickey of the Alaska Department of Fish and Game, and Mr Fredrik Thorsteinson and the late Robert Mahaffey of the U.S. Fish and Wildlife Service. Dr D. G. Chapman and Mr C. O. Junge Jr reviewed the manuscript.

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APPENDIX. Stream survey counts of pink salmon in Deadman and Uyak Rivers, Kodiak Island, Alaska. All figures tabulated are estimated numbers of pink salmon, in thousands.

TABLE A. Experiment No. 1, Aug. 19, 1957.

Airplane No.	Observer A				Observer C			
	7162		4590		7162		4590	
Counting unit	100	1000	100	1000	100	1000	100	1000
Stream section								
A + B	27.8	24	16.4	21	25.8	40	18.5	32
	26.0	32	17.5	19	24.6	43	14.8	26
AB	27.1	30	17.7	25	26.4	38	20.9	36
	29.1	26	17.7	19	28.2	36	17.9	27
C + D	8.1	10	8.3	10	6.0	9	7.6	17
	8.4	10	9.3	9	5.1	8	8.3	17
CD	8.8	9	8.6	10	5.2	14	10.6	19
	8.0	10	7.9	9	6.1	12	11.3	15

TABLE B. Experiment No. 2, Aug. 22, 1957.

Observer A					Observer C				Observer B			
Airplane No.	7162		4590		7162		4590		7162		4590	
Counting unit	100	1000	100	1000	100	1000	100	1000	100	1000	100	1000
Stream section												
A + B	18.7	19	17.7	20	16.2	20	14.6	24	13.7	14	11.0	12
	20.2	20	19.2	19	16.0	29	15.0	22	16.2	19	14.8	16
AB	19.0	17	19.1	19	15.6	28	13.2	21	8.0	17	14.3	23
	20.8	22	19.6	19	14.8	25	15.4	24	12.7	17	13.2	15

TABLE C. Experiment No. 3, Aug. 29, 1957.

Observer A				Observer D		Observer E	
Counting unit	100	1000		100	1000	100	1000
Stream section							
A + B		12.4	9	2.9	15	11.2	17
		11.7	10	5.0	11	5.3	18
AB		12.9	11	3.8	14	5.9	17
		10.0	9	3.9	11	5.3	14
C + D		6.9	8	4.1	6	4.7	10
		7.0	7	5.3	4	5.2	7
CD		7.2	7	4.6	6	4.5	11
		7.4	7	5.4	5	4.9	9

TABLE D. Estimated number of pink salmon on August 29, near the peak of the run (in thousands).

Observer A			Observer D	
Year	Deadman River	Uyak River	Deadman River	Uyak River
1956	25	10	23	21
	32	10	27	24
	20	9	23	25
	22	10	17	19
1957	8	11	6	14
	7	9	4	11
	7	9	6	15
	7	10	5	11
1958	14	7	17	12
	13	5	15	10
	12	6	19	12
	11	6	13	12

Preparation of Deoxynucleosides, Purine and Pyrimidine Bases and Deoxyribose 1-Phosphate from Deoxyribonucleic Acid Employing Salmon Enzyme Systems¹

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ABSTRACT

A crude enzyme system made by treating aqueous extracts of salmon kidney with protamine solution, followed by centrifugation to remove precipitated ribonucleic acid, was used to hydrolyze salmon deoxyribonucleic acid. When such hydrolyses were conducted in presence of toluene to minimize bacterial action, the deoxynucleosides of thymine, uracil, guanine and hypoxanthine were isolated in comparatively pure state. However, the digests also contained a significant proportion of unidentified non-nucleotide ultraviolet-absorbing substances. Digestions carried out in absence of toluene, with accompanying bacterial activity, resulted in formation of thymine, uracil, hypoxanthine and xanthine, which were isolated and characterized. A crude nucleoside phosphorylase enzyme was prepared from salmon livers by a method similar to that used with the kidney enzyme system. In presence of 0.2M KF it exhibited the following order of specificity: deoxyuridine > thymidine > deoxyguanosine > deoxycytidine > deoxyinosine > deoxyadenosine > uridine > cytidine > adenosine > inosine > guanosine > xanthosine. This preparation also exhibited marked phosphodeoxyribomutase and phosphoribomutase activities. Dicyclohexylammonium deoxyribose 1-phosphate was isolated in an amorphous form (purity 74%) from a reaction mixture containing thymidine, orthophosphate and the liver enzyme.

INTRODUCTION

IN RECENT YEARS fish muscle enzymes concerned with nucleic acid degradation have been studied extensively at this Station (Tarr, 1955; Tomlinson, 1958, 1959; Tomlinson and Creelman, 1960; Tomlinson and Warren, 1960; Tomlinson, Creelman and Reid, 1960), but information concerning the occurrence of such systems in other fish organs appears to be lacking. Consequently it was thought desirable to carry out a general study of the hydrolysis of deoxyribonucleic acid (DNA) by crude enzymes of certain salmon visceral organs, and of the phosphorylation of the deoxynucleosides derived therefrom to deoxyribose 1-phosphate.

MATERIAL AND METHODS

Purified, chromatographically homogeneous nucleosides, deoxynucleosides, purines and pyrimidines were purchased from the California Corporation for Biochemical Research, Los Angeles, (A grades). Dicyclohexylammonium salts of α -D-ribofuranose 1-phosphate (R1-P) and 2-deoxy-D-ribofuranose 1-phosphate (DR1-P) were analytically pure materials previously prepared in this laboratory (Tarr, 1958) which had been stored in vacuo at -20 to -30°C. The barium salts of α -D-ribofuranose 5-phosphate (R5-P) and 2-deoxyribose-D-ribofuranose

¹Received for publication January 26, 1961.

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5-phosphate (DR5-P) were prepared by known methods previously referred to (Tarr, 1959). D-ribose was purchased from the Nutritional Biochemicals Corporation, Cleveland, and 2-D-deoxyribose from the California Corporation for Biochemical Research. Dr Bernard Malin, Eli Lilly Inc., Indianapolis, kindly donated an ample supply of pure protamine sulphate.

Ribose was determined by the orcinol method (Mejbaum, 1939), deoxyribose by the Dische diphenylamine reaction as modified by Racker (1952) or by the Stumpf (1947) modification of the cysteine- H_2SO_4 acid reaction and total phosphorus by the method of Gomori (1942) after digestion with H_2SO_4 (Umbreit *et al.*, 1949). Orthophosphate, in presence of very acid labile DR1-P, was determined by the method of Friedkin (1950). The quantitative biuret reaction (Kingsley, 1939) was used to determine protein.

Kidneys, livers and ripe milts were removed from large red or white spring salmon (*Oncorhynchus tshawytscha*) or sockeye salmon (*O. nerka*) shortly after death and were promptly frozen in polyethylene bags in crushed CO_2 ice. The tissues were stored for several months at -30°C without noticeable loss of activity. However, it was found that kidneys obtained from non-eviscerated salmon which had been iced for a day or two retained only a small proportion of their ability to provide enzyme preparations capable of hydrolyzing DNA. Unless otherwise stated all procedures for isolation of the enzyme preparations used were carried out between 0 and 3°C .

EXPERIMENTAL

PREPARATION OF DNA

Since highly polymerized DNA was not required, the method of Jones (1920) for preparation of "thymus nucleic acid" (now known to be thymus DNA) was used with minor modifications as follows:

One kilogram of finely minced ripe milts (spring, sockeye, as well as chum salmon, *O. keta*, have all yielded successful results) was stirred into 2 l of H_2O containing 100 g sodium acetate and 33 g of NaOH, and the mixture heated for 2 hr on a boiling water bath with occasional stirring. The solution was centrifuged in stainless steel cups at 9500 g while still hot. Since the DNA tended to gel during centrifuging, the cups were immersed in a boiling water bath for a short time prior to decanting the supernate from the insoluble residue. The pale brown viscous liquid was adjusted, while still hot, to pH about 6.5 with 50% acetic acid. The solution was then poured slowly, with very rapid stirring, into 4 l of EtOH ($>99\%$). After standing overnight at 0°C the aqueous EtOH layer was carefully decanted, and the product dried, first by grinding with EtOH, and finally in vacuo over H_2SO_4 and solid KOH. The crude DNA was then dissolved in 300 ml of hot H_2O containing 2 g of NaOH and heated for 1 hr on a boiling H_2O bath. The suspended material was removed by filtration with suction through Whatman No. 1 paper on a steam-heated Büchner funnel and the clear viscous yellow liquid, after adjusting to pH 6.5 as above, was poured with rapid stirring into 600 ml of EtOH. After standing overnight the precipitated DNA was partially dried by grinding with several changes of EtOH. It was col-

lected on a Büchner funnel employing suction, washed with EtOH and diethylether and dried in vacuo as above. The yields obtained by this method were usually 50 to 55 g of a DNA containing about 7.5% P (purified high-viscosity DNA usually contains about 8.5% P).

PREPARATION OF A DNA-HYDROLYZING ENZYME SYSTEM FROM SALMON KIDNEY

Some 10 years ago it was found that salmon kidney usually contained appreciable amounts of deoxynucleosides as determined by a microbiological procedure (Tarr *et al.*, 1950), and therefore this organ was considered as a potential source of DNA-degrading enzymes. However, other organs were also examined as follows:

Small portions of frozen salmon visceral organs were blended with 2 volumes of water. The extracts were centrifuged 10 to 15 min at 14,000 *g* and filtered through a layer of glass wool to remove insoluble lipids and other floating debris. DNA (10 mg), MgSO_4 (0.02*M*) and 3 ml of tissue extract were incubated for 8 to 12 hr at 37°C, hydrolysis of DNA being followed by determination of orthophosphate at intervals by the Gomori procedure. The results indicated that the DNase activity of the tissues studied was in the following order of decreasing activity: kidney, heart, spleen, milt, pyloric caeca, liver and stomach. In view of these results kidney was selected for the following studies.

Kidney tissues of sockeye salmon have been found to contain rather high concentrations of DNA and RNA (Creelman and Tomlinson, 1959). Since the latter, if degraded, would probably yield ribonucleosides which would interfere with isolation of deoxynucleosides, the removal of RNA was obviously necessary with any procedure used for preparing a DNA-hydrolyzing enzyme system from kidney. Several methods for preparing such an enzyme were investigated.

Kidney tissue was blended with 2 volumes of water and the resulting mixture centrifuged 15 min at 12,000 *g* to remove insoluble material. When such extracts were autolyzed for 4 to 12 hr at 37°C, and then dialyzed for 16 to 24 hr against a solution (pH 7.0) containing both cysteine and MgCl_2 in 0.001*M* concentration to remove dialyzable degradation products of RNA, they had almost entirely lost their ability to hydrolyze DNA. Adjustment of such extracts to 0.9 saturation with ammonium sulphate at pH 7.0, collection of the precipitate either by centrifugation or overnight filtration through Whatman No. 31 paper, and dialysis as above yielded solutions which were devoid of DNase activity. Even dialysis of the kidney extracts without other treatment resulted in preparations which possessed only a fraction of their original activity.

In other experiments the aqueous kidney extracts were cautiously adjusted to pH 4.5 or 5.0 with 0.2*M* acetic acid and promptly centrifuged. The precipitates were immediately dissolved in 0.05*M* *tris*-(hydroxymethylaminomethane)HCl (*tris*-HCl) buffer pH 8.0. The solutions were practically free from RNA, as determined by the orcinol reaction, but possessed only feeble DNase activity. The neutralized supernatant solutions from the above precipitates also possessed only slight activity. These results indicated that at least one of the enzymes

responsible for degradation of DNA to yield deoxynucleosides and orthophosphate must be very sensitive to the above comparatively mild enzyme fractionation procedures. For this reason the following method, which appeared to cause no loss in specific activity, but which removed RNA successfully, was employed.

Salmon kidney (from spring or sockeye salmon in different experiments) was blended for about 1 min with 3 volumes of H_2O and the suspension centrifuged at 9500 *g* for 15 to 20 min. The supernate (pH about 6.5) was cautiously adjusted to pH 7.0 with 1*N* KOH and 1 volume of 2% protamine sulphate solution (adjusted to pH 5.5 with 1*N* H_2SO_4) was added for each 8 volumes of extract. The precipitate was removed by centrifuging and the clear supernate used immediately since it lost activity when stored at 0°C, also after being frozen (-30°C) and thawed.

The specific activity of these preparations was determined as follows: DNA (30 mg), 0.2 ml 1*M* tris-HCl buffer pH 7.5, $MgSO_4$ (0.02*M*) and 9 ml of enzyme preparation were incubated for 6 hr at 37°C, orthophosphate being determined at intervals by the Gomori method as an indication of DNA hydrolysis. The results obtained with two different preparations are given in Table I. Both

TABLE I. Preparation and specific activity of a DNA-hydrolyzing enzyme system from salmon kidney. A and B are different preparations.

Fraction	Volume		Protein N		Total units ³		Specific activity	
	A	B	A	B	A	B	A	B
	<i>ml</i>		<i>mg</i>				<i>units per mg protein N</i>	
Crude extract	160	285	68	153	32.6	61.8	0.48	0.403
Centrifuge supernate	150	272	51	130	26.6	57.8	0.52	0.445
Protamine treated	132	250	30.4	58	12.7	27.0	0.415	0.465

³Amount of enzyme preparation forming 1 μ mole of orthophosphate per hour at 37°C.

preparations had closely similar specific activities which were not increased by the fractionation procedure. Determination of ribose by the orcinol reaction showed that about 95% was removed by the protamine treatment. So far, no attempt has been made to separate the different enzymes probably involved in DNA degradation by these crude kidney enzyme preparations.

SALMON LIVER NUCLEOSIDE PHOSPHORYLASE

Previously a nucleoside phosphorylase which exhibited activity toward both purine nucleosides and deoxynucleosides but not toward the corresponding pyrimidine compounds was isolated from lingcod (*Ophiodon elongatus*) muscle (Tarr, 1958). Such enzymes carry out the general reaction:



and have therefore been used to prepare the natural (α) forms of the two pentose phosphate esters. In the case of R1-P, preparation of both biologically inactive (β) and active (α) forms has been achieved chemically (Wright and Khorana,

1956; Tener *et al.*, 1957). With DR1-P, chemical synthesis has as yet only resulted in mixtures containing different proportions of the α (active) and β (inactive) forms (MacDonald and Fletcher, 1960). The equilibrium in the above reaction is normally between 15 and 20% in favour of pentose 1-phosphate formation.

In connection with preparation of DR1-P in the present investigation the desirability of obtaining a pyrimidine deoxynucleoside phosphorylase was evident, since DNA degradation would yield both purine and pyrimidine deoxynucleosides, and the lingcod muscle enzyme exhibits no pyrimidine nucleoside phosphorylase activity. Accordingly, the principal visceral organs of salmon were examined to determine whether they exhibited pyrimidine deoxynucleoside phosphorylase activity.

Portions of the various organs were blended with 2 volumes of water, centrifuged, and the supernates tested as follows: Deoxyribonucleoside (0.1 ml containing 100 μ g of thymidine or deoxyuridine), 0.02 ml of 1M phosphate buffer pH 7.6 and 0.2 ml of tissue extract were incubated for 3 hr at 37°C. Ethanol (9 volumes) was added and the suspension centrifuged 5 min at 10,000 *g*. The supernates were evaporated to dryness over H₂SO₄ and solid KOH. The dry residues were mixed with 0.02 ml water and applied as a number of successive additions with intermediate drying to single starting zones on Whatman No. 1 paper. The papers were developed by descending chromatography for 16 hr at 20°C with *n*-propanol-28% NH₄OH-H₂O (6:3:1 v/v) (Hanes and Isherwood, 1949) and dried at room temperature. The papers were sprayed with aniline hydrogen phthalate reagent (Partridge, 1949) containing 0.5 ml of concentrated HCl per 100 ml and heated 5 min at 105°C. The presence of both DR5-P and DR1-P was verified by appearance of bright yellow zones which fluoresced strongly in ultraviolet light. These esters moved about 6 and 8 cm respectively under the chromatograph conditions and were not well separated when applied to the paper in crude solution. DR5-P presumably arises as a result of phosphodeoxyribomutase activity. The results of these preliminary tests indicated that the salmon liver preparations were most active with both substrates. Some activity was observed with kidney and spleen extracts, but none with heart, stomach or pyloric caecae.

Since liver appeared to afford the best source of a pyrimidine nucleoside phosphorylase, a purification procedure was sought. Initially, centrifuged aqueous extracts of blended spring or sockeye salmon livers (1 part of liver to 3 of H₂O) were assayed for thymidine phosphorylase activity according to the modified procedure of Friedkin and Roberts (1954a) in which liberation of thymine from thymidine is measured by the optical density of clarified alkaline solutions at 300 *m* μ . When four different concentrations of extract (0.02 to 0.08 ml) were incubated at pH values of 6.0 and 7.0 for 2 hr at 37°C in a final volume of 1.1 ml using this assay procedure, it was found that the specific activity was between 1.6 and 1.7 (calculated as μ moles of thymine formed per hour per milligram of protein nitrogen).

Attempts to purify the liver nucleoside phosphorylase by ammonium sulphate fractionation of aqueous extracts at pH 7.0, followed by dialysis against 0.001M cysteine and MgCl_2 (at pH 6.5), or by fractionation at pH 4.5 or 5.0 using dilute acetic acid, yielded preparations which were either inactive or had specific activities considerably lower than those of the crude extracts. Dialysis of freshly prepared extracts against H_2O , 0.1M NaCl, 0.1M sodium acetate (pH 6.7), 0.1M *tris*-HCl buffer pH 7.0, 0.05M KCl in 0.01M veronal buffer pH 7.4 or 0.05M KCl containing 0.001M MgCl_2 at 0°C for 3 hr caused from 40 to 50% loss of activity as judged by the above assay procedure. After a 16-hr dialysis the preparations had lost all measurable activity while a non-dialyzed control was still fully active.

In view of these results a simple rapid procedure was developed which yielded a heterogeneous preparation adequate for some preliminary studies on the enzyme, and for preparation of DR1-P.

Thawed livers of spring or sockeye salmon which had been obtained from fish shortly after death, and which had been stored several months at -30°C, were used. The liver was cut into small pieces and blended at about 0°C with 2 volumes of water and KF sufficient to bring the final concentration to 0.2M. In a typical experiment 100 g of liver was blended with water (200 ml) and KF (5.65 g) at high speed in a Serval Omni-Mixer for 1 min. The suspension was centrifuged at 40,000 g for 15 min, and the supernate (pH 6.2) poured through a thick pad of fine glass wool to remove floating particles (chiefly lipid material) (yield 220 ml). The solution was mixed with 37 ml of 2% protamine sulphate solution (pH 5.5) and centrifuged 15 min at 25,000 g to yield 252 ml of clear red supernate (pH 6.0). Such preparations may be frozen and stored for at least a month at -30°C without any serious loss in activity.

Initial attempts to determine the specificity of this crude liver enzyme by measuring liberation of orthophosphate from DR1-P in presence of various pyrimidine or purine bases were not very successful. The large amount of protein in the crude preparations rendered the determination of orthophosphate in the presence of very acid labile DR1-P by the method of Friedkin (1950) rather unsatisfactory. For this reason present experiments were confined to a study of formation of DR1-P from known deoxynucleosides and nucleosides using paper chromatographic separation.

Deoxynucleoside (20 μ moles), 1M potassium phosphate buffer pH 7.0 (0.02 ml) and enzyme (2.0 ml) were incubated for 2 hr at 37°C in small glass test tubes. The pH of the reaction mixture was 7.0. After adding 0.08 ml of 0.1N KOH to bring the pH to about 8.0, the tubes were immersed in a boiling water bath for 3 min with stirring, promptly chilled, and the protein coagulum was removed by filtering through a small conical Whatman No. 1 paper, the coagulated protein being washed with four successive 0.5-ml portions of water. The clear filtrates were evaporated to dryness in 5-ml beakers in an evacuated desiccator over concentrated H_2SO_4 and solid KOH. The residues were dissolved in 0.1 ml of water, and the resulting solution, followed by the washings obtained by rinsing the beakers with a further 0.1 ml of water, streaked along a 12-cm starting line on a 15-cm wide Whatman No. 3 mm paper, using several successive applications with

intermediate drying. The papers were subjected to descending chromatography for 20 hr at 20°C using *n*-propanol-28% NH_4OH - H_2O (6:3:1 v/v). After drying at room temperature a 2-cm wide strip was cut lengthwise from each paper (this represented approximately 16.7% of the material applied). After an examination with ultraviolet light to ensure that deoxynucleosides or nucleosides would not interfere with determination of pentose phosphates, the strips were sprayed first with aniline hydrogen phthalate (Partridge, 1949) and, after drying, heated with phosphomolybdic acid reagent (Hanes and Isherwood, 1949). In this chromatographic system, when purified preparations are used, DR1-P, DR5-P, R5-P and orthophosphate are all separated, the rapidity of their migration being approximately in the above order. R1-P moves at about the same rate as DR5-P. The rates of flow are all reduced when the esters are applied in a rather crude mixture as in the above experiment, and separations are also poorer. Thus there was no clear-cut separation of DR1-P and DR5-P or of R1-P and R5-P, though it was possible to distinguish the individual compounds in the mixtures by application of both the aniline hydrogen phthalate and phosphomolybdic acid sprays.

The zones corresponding to DR1-P plus DR5-P (about 7 cm from origin), and also those corresponding to the ribose phosphates, were cut out as a 3-cm-wide strip and eluted into 10 ml of water for 1 to 2 hr. The eluates were assumed to represent 83.3% of the expected recovery and allowance was made for this in the calculations. Determinations of deoxyribose and ribose were used as indices of the amount of DR1-P and R1-P formed. The results (Table II) showed that

TABLE II. DR1-P and R1-P formation by salmon liver nucleoside phosphorylase.

Substrate	$\mu\text{moles of:}$	Amount formed ⁴	Results of visual examination of sprayed paper strips
	Deoxyribose phosphates ⁵		
Deoxyuridine	5.00	25	++++
	4.62	23	++++
Thymidine	2.8	14	+++
Deoxycytidine	0.77	3.9	++
Deoxyguanosine	0.79	4.0	++
Deoxyinosine	0.66	3.3	++
Deoxyadenosine	0.58	2.9	+
	Ribose phosphates		
Uridine	0.47	2.35	+++
Cytidine	0.25	1.25	++
Guanosine	0.042	0.21	-
Inosine	0.054	0.27	-
Adenosine	0.068	0.34	+
Xanthosine	0.04	0.20	-

⁴Percentage of the 20 μmoles of each substrate used.

⁵The figures given represent the sum of deoxyribose (or ribose) 1- and 5-phosphate esters and are averages of duplicate determinations after subtracting appropriate controls obtained by running experiments without added nucleosides.

the enzyme preparations exhibited deoxyriboside and riboside phosphorylase activity, and that this activity was roughly ten times greater with deoxyribosides under the experimental conditions. The pyrimidine compounds (with the exception of deoxycytidine) were much better substrates than the purine compounds.

These results indicate the very wide specificity of the enzyme preparation. However, since the preparation has not yet been purified, it is possible that more than one nucleoside phosphorylase system may be involved. In this connection it is of interest that horse liver deoxynucleoside phosphorylase is apparently a single enzyme (Friedkin, 1950; Friedkin and Roberts, 1954a and b), which synthesizes deoxynucleosides from thymine, uracil, hypoxanthine and guanine in presence of DR1-P.

PHOSPHOPENTOSEMUTASE ACTIVITY OF THE NUCLEOSIDE PHOSPHORYLASE

The above experiments showed that the crude salmon liver nucleoside phosphorylase preparation was able to form pentose 5-phosphates from the corresponding pentose 1-phosphate esters, and therefore contained both phosphoribomutase and phosphodeoxyribomutase activities. The rate of formation of DR5-P from DR1-P was determined as follows:

A reaction mixture containing 100 μ moles of thymidine, 0.1 ml of 1M potassium phosphate buffer (pH 7.0) and 9.9 ml of crude nucleoside phosphorylase enzyme was incubated at 37°C, 1.0-ml samples being removed at intervals and heated immediately for 3 min in a boiling water bath. The samples were then treated as in the previous experiment. The zones on the chromatograms which corresponded to DR5-P and DR1-P (about 6 and 8 cm from origin) were eluted together into 10 ml of water. After 2 hours standing with occasional mixing, deoxyribose, labile phosphorus (Gomori method) and "total phosphorus" (after heating samples for 45 minutes at 100°C in 0.1N H₂SO₄ in order to hydrolyze the more acid stable DR5-P) were determined, using appropriate duplicate aliquants. The results (Table III) showed that there was comparatively rapid

TABLE III. Rate of formation of DR1-P and DR5-P from thymidine.

Time	Deoxyribose	Total P	Labile P	Ratio of deoxyribose to total P ⁶	DR1-P ⁷	DR5-P ⁷
<i>minutes</i>	μ moles	μ moles	μ moles			
0	*	*	*	—	—	—
15	1.40	1.25	0.89	1:0.89	71	29
30	1.35	1.24	0.66	1:0.92	53	47
60	1.37	1.25	0.62	1:0.91	49	51
120	1.34	1.58	0.51	1:1.15	37	63
180	1.05	1.16	0.34	1:1.10	29	71
240	1.10	0.97	0.11	1:0.88	11	89
480	1.12	1.20	0.11	1:1.08	9	91

⁶Theoretical ratio is 1:1.

⁷Calculated from the difference between acid labile and total phosphorus.

* = Not appreciable.

formation of DR1-P since 1.4 μ moles of deoxyribose phosphates (i.e. 14% of the 10 μ moles of thymidine used) were formed within 15 min. Thereafter there was a slow increase in the proportion of DR5-P, the final equilibrium being about 90% in favour of this more acid-stable ester. This value is similar to that reported for phosphoribomutase in the literature, and that recently found for lingcod muscle phosphoribomutase (Martin and Tarr, 1961).

PREPARATION OF DEOXYNUCLEOSIDES

The method used was based on that described by Anderson *et al.* (1952). Initial experiments showed that since DNA hydrolysis was comparatively slow, it was necessary to retard bacterial growth. Under the conditions used (pH about 7.5 at 37°C) chlortetracycline (10 μ g/ml) proved unsatisfactory due to its instability and toluene was therefore employed as a bacteriostat.

In one experiment 11 g of DNA (6.6% P) was dissolved in 200 ml of hot water and added, together with 49 g $\text{Mg}_2\text{SO}_4 \cdot 7\text{H}_2\text{O}$ (0.02M final concentration) to 3.8 l of crude protamine-treated salmon kidney enzyme preparation, the pH of which had been cautiously adjusted to 7.6 with 1N KOH. The initial orthophosphate content (121 μ g/ml) rose to 226 μ g/ml during a 30-hr incubation at 37°C under a layer of toluene. This indicated formation of 420 mg of orthophosphate, equivalent to 58% hydrolysis of the DNA. In a second similar experiment 15 g of DNA (7.58% P) was hydrolyzed under the above conditions with 4.2 l of kidney enzyme in a total volume of 4.4 l for 45 hr at 37°C. The orthophosphate concentration increased from 136 to 268 μ g/ml, equivalent to formation of 580 mg of orthophosphate or 51% hydrolysis of the DNA.

The two preparations were pooled, filtered by gravity through Whatman No. 31 paper, and evaporated, using a rotary evaporator (37°C), to a viscous brown liquid (about 60 ml). Ethanol (340 ml) was added with stirring and the slurry (85% EtOH content) shaken overnight at 25°C. The suspension was centrifuged at 9500 *g* and the supernate set aside. The residue was mixed with sufficient water to bring the volume to about 60 ml, and again extracted with EtOH (340 ml) for 4 hr by shaking. The centrifuging and extraction were repeated once more, and the alcohol extracts were pooled.

The combined extracts were evaporated under reduced pressure as above to a thick syrup. The syrup was diluted with water to 150 ml and mixed with 75 g of acid-washed Norit A charcoal (Pfanstiel Labs. Inc., Waukegan, Ill.). The deoxynucleosides (which are quantitatively adsorbed) were eluted from the charcoal on a 15-cm-diameter Büchner funnel with 8 l of 50% EtOH containing 1% of 28% NH_4OH employing suction. This procedure removed all but two free amino acids (presumably aromatic compounds) which occurred in the digest and were adsorbed by the charcoal. These two amino acids appeared later in the eluate from the Dowex 2 $\times$ 8 formate column (see below).

The charcoal eluate was evaporated as above, the pH adjusted to 10.5 with 28% NH_4OH solution, and the solution (340 ml) filtered through Whatman No. 1 paper. The clear yellow solution was run by gravity on to a 200–400-mesh

Dowex 2×8 formate resin column 32 cm long and 2.8 cm diameter, and the column was washed with 500 ml of water. It was eluted under slight pressure at 250 ml/hr employing a gradient in which 12 l of 0.4*M* ammonium formate (pH 8.6) was run into 12 l of water which was adjusted to pH 9 with NH_4OH . Twenty-millilitre fractions were collected and checked for absorption at 260 $\text{m}\mu$ (after appropriate dilution) and for their deoxyribose content (0.1-ml portions using the cysteine- H_2SO_4 method). The results are shown in Fig. 1.

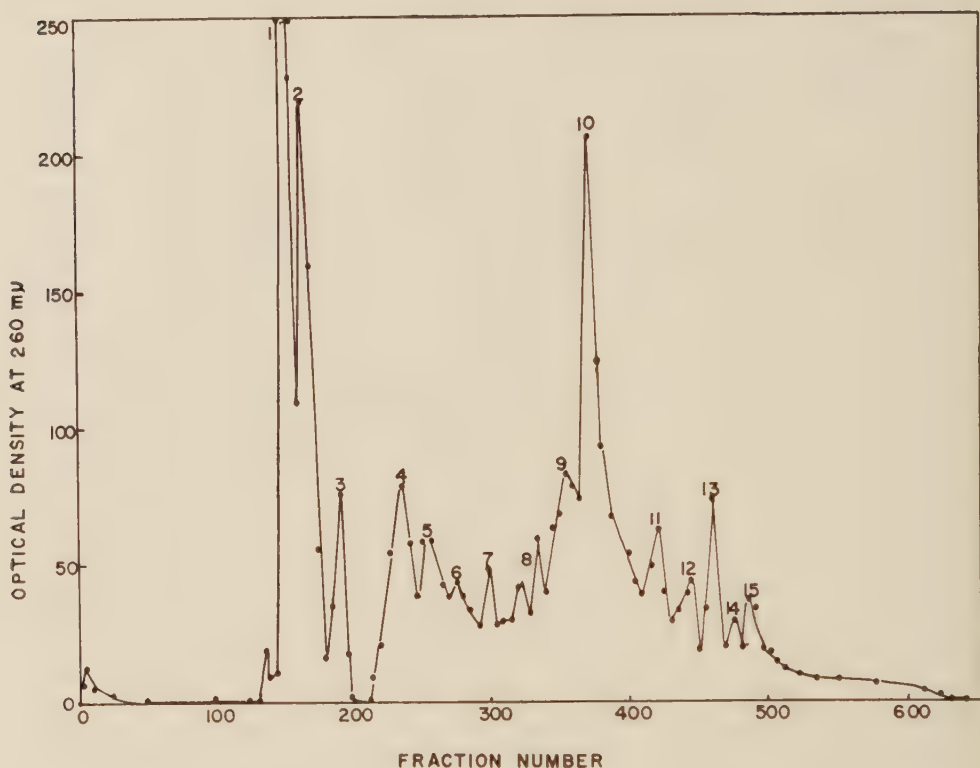


FIG. 1. Separation of deoxynucleosides on a Dowex 2 × 8 formate column.

In Fig. 1, Peak 1 (O.D. at 260 $\text{m}\mu$ was 290) contained thymidine and Peak 2 deoxyuridine. Peak 3 was an amino acid (unidentified). Peak 4 contained both guanine and hypoxanthine deoxyribosides, and Peak 5 hypoxanthine deoxyriboside. All fractions between 139 and 175 and between 215 and 280 contained deoxyribose, the remainder being deoxyribose-free. The fractions indicated under Peaks 7 to 15 inclusive were pooled so that nine solutions were obtained. These will be referred to later.

The fractions noted above which comprised Peaks 1 to 6 were pooled as indicated in Table IV and the five solutions thus obtained were evaporated to small volumes which were set aside at 0°C to permit crystallization of the deoxynucleosides or amino acids. Data concerning the isolation of these compounds are

given in Table IV. All absorption data are given in $m\mu$. Thymidine was recrystallized once from anhydrous methanol. Deoxyuridine, which was contaminated with an amino acid, was purified as follows. The pooled fractions, after removing most of the water using a rotary evaporator, were dried in high vacuum over P_2O_5 . The residue was ground with 10 ml of anhydrous methanol

TABLE IV. Preparation of deoxynucleosides.

Fraction No. ⁸	Crystallization volume	Yield of product	O.D. ratios ⁹ in 0.01N HCl		Purity: calc. ¹⁰ from ϵ max. in 0.01N HCl	Compound
			250/260	280/260		
1 (145-160)	<i>ml</i>	<i>mg</i>			<i>%</i>	
	10	1,100	0.65 (0.65)	0.75 (0.72)	90 (267)	Thymidine
	recrystallized from 10 ml methanol	900	0.62 (0.65)	0.71 (0.72)	101 (267)	"
	filtrate evaporated to 5 ml yielded a crystalline residue at 0°C.	475	—	—	—	Amino acid unidentified
2 (161-180)		1,770	0.76 (0.72)	0.38 (0.37)	60 (262)	Deoxyuridine
	recrystallized	505	0.73 (0.72)	0.35 (0.37)	97.5 (262)	"
	O.D. ratios in 0.01N NaOH		0.825 (0.81)	0.34 (0.31)		
3 (181-200)	150	200	—	—	—	Amino acid unidentified
4 (201-245)	150	240	1.63 (1.63)	0.19 (0.23)	83 (249)	Hypoxanthine deoxyriboside
	75 (filtrate)	350	0.98 (1.02)	0.71 (0.70)	65 (255)	Guanine deoxyriboside
	Contaminating ammonium formate was removed under high vacuum at 45°C.					
		215	0.98 (1.02)	0.71 (0.70)	95 (255)	Guanine deoxyriboside
5+6 (246-290)	50	620	—	—	57 (249)	Hypoxanthine deoxyriboside
	Contaminating ammonium formate removed under high vacuum at 45°C.					
	50	300	1.62 (1.63)	0.18 (0.23)	90 (249)	"

⁸Fractions which were pooled are given in parentheses.

⁹The values in parentheses are those given by the California Corporation for Biochemical Research, Los Angeles, in a chart on "Properties of the nucleic acid derivatives".

¹⁰The wave length used in calculating the ϵ max. values is given in parentheses.

and the crystalline residue (amino acid) removed by filtration. The filtrate was evaporated under reduced pressure to a gum (1.77 g) (Table IV). The gum was dissolved in 5 ml of warm methanol, applied to eight 46-cm sheets of washed Whatman 3-mm paper in long streaks and developed (descending 16 hr at 20°C) successively as follows with intermediate drying. (A) 1% of 28% ammonium hydroxide in water-saturated *n*-butanol, 16 hr. (B) *n*-propanol, 28% ammonium

hydroxide, water (6:3:1 v/v). The deoxyuridine which was well separated from a contaminating amino acid and traces of other ultraviolet-absorbing compounds was eluted from the paper strips with 90% EtOH. The eluates were dried under reduced pressure (rotary evaporator) and the deoxyuridine crystallized, after drying over P_2O_5 , from 2 ml of anhydrous methanol at 0°C. All four deoxynucleosides were isolated in comparatively pure state and were identified by their characteristic ultraviolet absorption spectra, their O.D. ratios at 250/260 and 260/280, their absorption maxima, and finally by their chromatographic properties in three solvent systems (Table VI).

The fractions representing Peaks 7 to 15 inclusive (Fig. 1) were pooled, evaporated under reduced pressure to small volumes, and the ammonium formate was removed under high vacuum at 45°C (Anderson *et al.*, 1952). Fraction 7 yielded 40 mg of hypoxanthine (about 85% purity) O.D. ratios 250/200 = 1.47; 260/280 = 0.059 (0.04) and fraction 8 yielded 100 mg of hypoxanthine of similar purity as judged spectroscopically.

The pooled fractions composing Peaks 9 to 15, which were first assumed to be deoxynucleotides from their chromatographic behaviour, were not identified. When small amounts (1 to 10 O.D. units at 260 $m\mu$) were subjected to electrophoresis in 0.05M sodium citrate buffer pH 3.5, using Whatman No. 3 paper (30 v/cm), these seven peaks each yielded two to five separate ultraviolet-absorbing substances which migrated anodically from 2 to 14 cm in 2 hr. The distances travelled are similar to those exhibited by nucleoside mono-, di- and triphosphates toward the cathode under the same conditions. On chromatography in *iso*-propanol-28% NH_4OH-H_2O (7:1:2 v/v) (Razzell and Khorana, 1959), the peaks yielded from two to five distinct ultraviolet-absorbing zones (Rf values between 0.3 and 0.6). A number of these electrophoretically or chromatographically separated substances were eluted from the paper with 0.01N HCl and their absorption in the ultraviolet region was determined as usual. While absorption was quite high in the range 230 to 280, none of the substances gave O.D. ratios 250/260 and 280/260 which were at all typical of known purines, pyrimidines or their nucleoside or nucleotide derivatives. Thus the following ratios (250/260 and 280/260 respectively) were recorded for major ultraviolet-absorbing zones from electrophorograms: Peak 9, 0.85 and 0.75; Peak 10, 0.75 and 0.79; Peak 12, 0.88 and 0.77; and Peak 13, 1.29 and 0.52. The eluates of several typical zones both from electrophorograms and paper chromatograms gave negative tests for deoxyribose (Stumpf, 1947) and none contained measurable phosphorus after H_2SO_4 hydrolysis (Umbreit *et al.*, 1949). No further attempts were made to identify these substances.

PREPARATION OF PURINES AND PYRIMIDINES

It was noticed that when digests similar to the above were incubated in absence of toluene, bacterial action commenced after about 8 to 10 hr and was severe after 16 hr. In digests so prepared, deoxyribose, as determined by the Dische reaction, was usually either absent or present in comparatively small amounts, indicating that hydrolytic (or phosphorolytic) cleavage of the deoxy-

nucleosides had occurred. Paper chromatography showed that such extracts contained free purines and pyrimidines, and could therefore be used as a source of these bases. Two such digests were prepared and used for isolation of purines and pyrimidines as follows, the general conditions being those employed in preparing the deoxynucleosides except that no toluene was used.

In one experiment, 17 g DNA (6.1% P) was dissolved in 200 ml of hot water and incubated for 5 hr at 37°C with 5 l of kidney enzyme and MgSO_4 in 0.02*M* concentration. The mixture was then allowed to stand for 16 hr at 22°C. In another experiment 14 g DNA (7.5% P) was incubated with 4.6 l of enzyme for 12 hr at 37°C followed by gradual cooling for 8 hr at 0°C. Analyses indicated that 90% of the DNA-P had been liberated as orthophosphate in the first experiment, and 87% in the second. Both extracts emitted unpleasant odours indicative of incipient bacterial putrefaction. The solutions were evaporated, extracted with 85% EtOH, charcoal treated and subjected to Dowex 2 $\times$ 8 formate chromatography under the same conditions as those employed in the isolation of the deoxynucleosides. The results are given in Fig. 2 and Table V. Thymine, uracil,

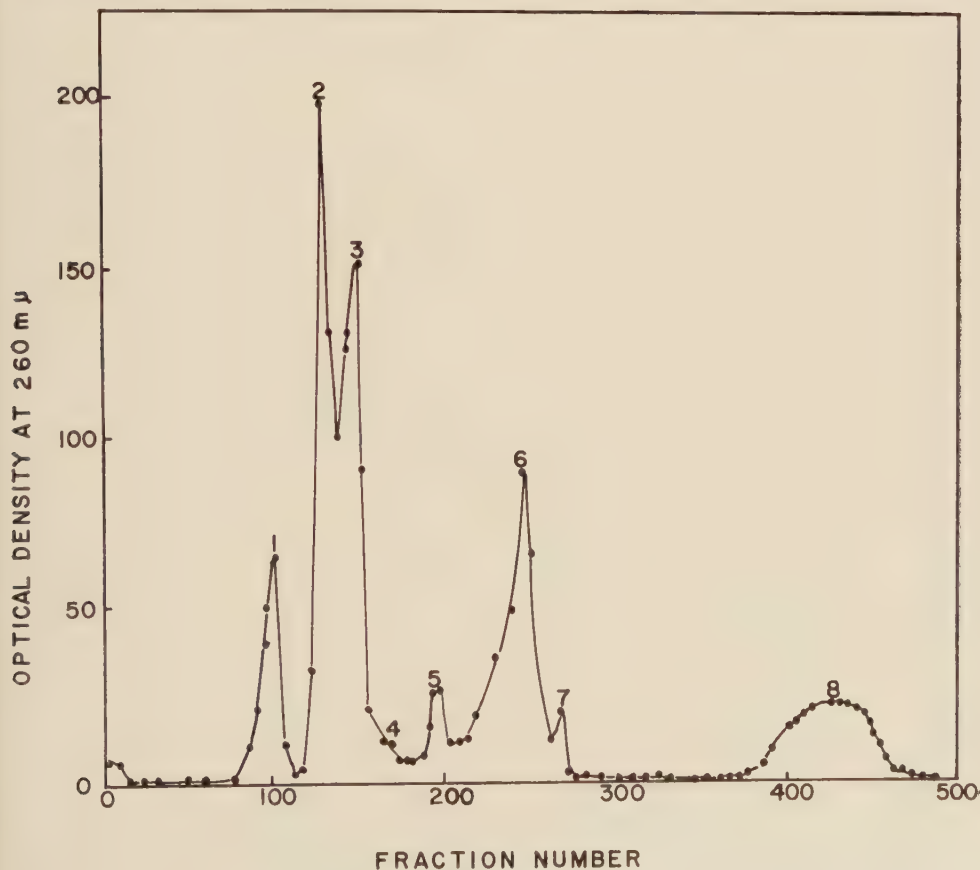


FIG. 2. Separation of purines and pyrimidines on a Dowex 2 $\times$ 8 formate column.

TABLE V. Preparation of purines and pyrimidines.

Fraction No. ⁸	Crystallization volume (ml)	Mg of product	O.D. ratios ⁹ in 0.01N HCl		% Purity; calc. ¹⁰ from ϵ max. in 0.01N HCl	Compound
			250/260	280/260		
1 (75-110)	10	40	—	—	—	Amino acid (unidentified)
2 (115-140)	50	375	0.69 (0.67)	0.50 (0.53)	95 (264)	Thymine
3	20	75	0.70 (0.67)	0.48 (0.53)	95 (264)	Thymine
4	80	160	0.88 (0.84)	0.17 (0.17)	94 (259)	Uracil
(141-145)	25	80	0.85 (0.84)	0.17 (0.17)	89 (259)	Uracil
5 (156-175)	35	110	—	—	—	Amino acid (unidentified)
6 (176-205)	10	180	1.61 (1.63)	0.20 (0.23)	93 (259)	Hypoxanthine deoxyriboside
7 (206-247)	45	370	1.44 (1.45)	0.057 (0.04)	94 (248)	Hypoxanthine
8 (248-270)	20	145	1.47 (1.45)	0.52 (0.04)	90 (248)	Hypoxanthine
9 (370-480)	90	115	0.53 (0.56)	0.59 (0.6)	93 (267)	Xanthine

Footnotes as in Table IV.

hypoxanthine and xanthine (presumably arising from guanine deamination) were isolated in a reasonably pure state as judged by their ultraviolet absorption spectra, their paper chromatographic properties in three solvent systems (Table VI) and their " ϵ max." values. A small amount of hypoxanthine deoxyriboside was also obtained and, as with the deoxynucleoside preparations, two unidentified amino acids.

TABLE VI. Rf values of isolated deoxynucleosides, purines and pyrimidines compared with reference compounds (about 50 μ g of each chromatographed). Rf values at 20°C in three solvent systems¹¹ using Whatman No. 1 paper. A = compound isolated. B = reference compound.

	1		2		3	
	A	B	A	B	A	B
Thymine	.68	.68	.74	.72	.715	.715
Thymidine	.78	.77	.87	.89	.63	.63
Uracil	—	—	.82	.80	.54	.54
Deoxyuridine	.74	.74	.83	.83	.51	.51
Deoxyguanosine	.52	.55	.79	.80	.54	.54
Hypoxanthine	—	—	.62	.62	.56	.57
Deoxyinosine	.70	.70	.82	.825	.53	.53
Xanthine	—	—	.62	.62	—	—

¹¹1 = 2-hour ascending development in 5 ml *iso*-propanol + 5 g. (NH₄)₂SO₄ + 100 ml water (Friedkin, 1955). 2 = 2-hour ascending development in ammonia water pH 10.0 (Wyatt, 1955). 3 = 16-hour descending development in *iso*-butyric acid, 75; water, 25; and 28% ammonia hydroxide, 1.3 (v/v).

PREPARATION OF DEOXYRIBOSE 1-PHOSPHATE

In previous work (Tarr, 1958) DR1-P was prepared in good yield using deoxyguanosine as substrate. The liver nucleoside phosphorylase described above exhibited greatest activity with the pyrimidine deoxynucleosides of uracil and thymine as substrates, and therefore an investigation of the formation of DR1-P with this enzyme was undertaken. Initial studies in which reaction mixtures containing 10 μ moles of thymidine and orthophosphate per millilitre of crude salmon liver nucleoside phosphorylase (3.9 mg of protein N per ml) showed that the enzyme had a specific activity corresponding to about 0.025 μ mole of DR1-P formed per minute per milligram of protein N at 37°C. One major difficulty with this enzyme was occasioned by the presence of the phosphodeoxyribomutase activity, which has so far not been eliminated. DR1-P and DR5-P are difficult to separate by ion-exchange chromatography unless borate complexing is employed. Consequently, in the present work conditions were employed which would tend to minimize DR5-P formation, and, since this compound does not form a crystallizable dicyclohexylammonium salt, advantage was taken of this fact in isolation of DR1-P.

Two millimoles (484.5 mg) of thymidine prepared from salmon DNA, 50 ml of crude salmon liver nucleoside phosphorylase and 1.5 ml of 1M potassium phosphate buffer pH 7.0 were incubated for 40 min at 37°C. After adding 0.5 ml of 28% NH_4OH the mixture was heated to 90°C in a boiling water bath, chilled to 0°C, the protein removed by filtration and the residue washed on the funnel with 100 ml of water. The combined filtrates were evaporated to 15 ml using a rotary evaporator (37°C) and passed through a 200–400-mesh Dowex 50 $\times$ 8 NH_4^+ ion-exchange resin column 10 cm long and 1.9 cm diameter. The column was washed with 100 ml H_2O , the eluate and washings were evaporated to approximately 2 ml under reduced pressure (pH > 7.0) and 6 ml of 28% NH_4OH and 12 ml of *n*-propanol were added. After shaking mechanically for 1 hr the suspension was filtered through Whatman No. 4 paper on to the top of a 27- by 3.4-cm cellulose powder column. This column was prepared by suspending 75 g of Whatman ashless cellulose powder in a solution containing *n*-propanol–28% NH_4OH – H_2O (6:3:1 v/v) and packing this in layers, as usual. The column was washed with 500 ml of the solvent before applying the above solution, and was eluted with the same solvent at a flow rate of 1.4 ml/min, collecting 12.5-ml fractions. The fractions were assayed for deoxyribose (Stumpf method) and labile P (Gomori method) using 0.1-ml portions from which the solvent was removed in vacuo before making the determinations. Fractions 15 to 25 inclusive which gave strongly positive tests for deoxyribose but not for labile phosphorus were pooled and evaporated to dryness. The residue was dissolved by warming in 10 ml of anhydrous methanol, filtered and set aside at 0°C. The crystalline mass was collected on a tared sintered glass filter (yield 260 mg). The O.D. ratios were: 250/260, 0.65; and 250/280, 0.71; which are characteristic of thymidine. The purity as calculated by the “ ϵ max.” when dissolved in 0.01N HCl was 97%.

Fractions 27 to 31 inclusive gave positive tests for both deoxyribose and labile phosphorus. There was some indication of slight separation of deoxyribose 1- and 5-phosphates but this was not sufficient to permit clear-cut separation. The fractions were pooled, and, after adding 1 millimole of barium acetate, were evaporated to dryness under reduced pressure. The dry product was taken up in 5 ml of water. The insoluble residue was removed by centrifuging, washed with water, the solutions were pooled and 30 ml of EtOH was added, care being taken to keep the pH above 7.0. The precipitate was collected by centrifuging, suspended in 80% EtOH, centrifuged and dried 3 hr over P_2O_5 in high vacuum. The yield was 122 mg of crude mixed barium salts of deoxyribose 1- and 5-phosphates. Analysis for deoxyribose, labile and total phosphorus indicated that the material contained only 43% of the theoretical amounts (calculated on the basis of MW = 350) and that about 23% occurred as DR5-P and 77% as DR1-P. When a small portion of the crude material was examined by paper chromatography after removing the barium by means of Dowex 50 $\times$ 8 NH_4^+ resin, both DR1-P and DR5-P were identified.

The crude barium salt was dissolved in 5 ml of H_2O and filtered through Whatman No. 4 paper on to a 200–400-mesh Dowex 50 $\times$ 8 cyclohexylamine ion-exchange column 5 cm long and 1.9 cm diameter, the filter and column being washed with 25 ml of water. The column eluate was evaporated to dryness using a rotary evaporator (30°C). The residue was dissolved in 1.0 ml water-saturated *n*-butanol and diethyl ether (4 ml) was added gradually at 0°C. Crystallization did not occur. The pale yellow precipitate was dried in high vacuum over P_2O_5 after the solvent was decanted. The yield was 36 mg. Analysis showed that the material contained 74% of the expected amount of deoxyribose, 73% of the total phosphorus and 71% of labile phosphorus expected for dicyclohexylammonium DR1-P (MW 412). Only a single zone corresponding to DR1-P was found by paper chromatography, DR5-P being absent.

In a second preparation 1.15 g of crude mixed deoxynucleoside syrup (alcohol extraction step from a DNA digest) was incubated for 1 hr at 37°C with 100 ml of liver enzyme and excess orthophosphate. In this case the ion-exchange resin isolation procedure employed in previous work (Tarr, 1958) was used. Only 90 mg of crude mixed barium deoxypentose phosphate salts of about 47% purity as calculated by the deoxyribose and total phosphorus content was obtained. This material contained about 30% of DR5-P and 70% DR1-P as determined by the ratio of labile to total phosphorus, and gave two distinct zones characteristic of these esters on paper chromatography. The product was not further purified.

DISCUSSION

Recent reviews have summarized present knowledge regarding enzymic hydrolysis of DNA (Schmidt, 1955; Laskowski, 1959). The lability of the salmon liver crude enzyme preparation used in the present studies has complicated purification. Thus the possible participation of a number of enzymes such as a

DNA depolymerizing endonuclease, of phosphodiesterase enzymes yielding either 3'- or 5'-deoxymononucleotides (Tener *et al.*, 1959) and of phosphomonoesterases remains to be determined. Where bacterial contamination was largely avoided by use of toluene the important end products of action of the crude kidney enzyme on DNA were deoxynucleosides. The nature of the ultraviolet-absorbing fractions which were eluted subsequent to the purines, pyrimidines and deoxynucleosides was not determined. Deoxynucleotides were not found in these fractions.

Salmon liver nucleoside phosphorylase was found to activate a wide range of nucleosides. However, its activity was greater toward the pyrimidine compounds deoxyuridine and thymidine than toward the other substrates studied. The enzyme showed the following order of activity toward other deoxynucleosides investigated: deoxyguanosine > deoxycytidine > deoxyinosine > deoxyadenosine > uridine > cytidine > adenosine > inosine > xanthosine. In this connection it is interesting to note that Friedkin (1950) found that horse liver thymidine phosphorylase exhibited activity toward both inosine and adenosine, as well as toward thymidine.

Salmon liver nucleoside phosphorylase exhibited an instability similar to that found with the kidney DNase enzyme preparation. However, the enzyme worked actively with no sign of hydrolytic activity toward the nucleoside substrates (i.e. no detectable free deoxyribose or ribose formation) in presence of 0.2M KF. Perhaps KF could be used as a stabilizing agent during purification. This enzyme preparation also possessed both phosphoribomutase and phosphodeoxyribomutase activity which complicated attempts to isolate DR1-P from reaction mixtures. Attempts to prepare this ester in pure crystalline form were unsuccessful, though it was isolated as an amorphous product about 74% pure. The original preparation method of Friedkin, which gave good preparations with the horse liver enzyme, was not studied. In any case, much better yields of both crystalline deoxyribose 1-phosphate and ribose 1-phosphate dicyclohexylamine salts can be obtained with lingcod muscle nucleoside phosphorylase (Tarr, 1958).

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A Comparison of Three Methods of Inactivating Lobster Claws¹

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ABSTRACT

Mortalities during 4½ months among 4 lots of 50 lobsters, 3 with claws inactivated, were: plugged 54%, banded 56%, cut tendons 78%, untreated 98%. No appreciable loss of claws, bands or plugs occurred. Plugged lobsters are more susceptible than banded to infection with *Gaffkya homari*, the agent causing lobster blood disease. The advantages of banding outweigh the disadvantages.

INTRODUCTION

TO REDUCE injuries and mortalities among live lobsters during storage and shipment, the crusher claw or both claws are inactivated. In Europe this is accomplished by fastening twine, brass wire or rubber bands around the claws (Thomas, 1958). In North America the most common method is to insert a small wooden or plastic plug in the thumb joint. In a few areas some fishermen cut the extensor tendons so the lobsters are unable to open their claws. Rubber bands are also used to a limited extent.

Each of these methods has certain advantages and disadvantages. Plugging is effective, cheap and fast. In time, however, the tissue near the plug turns dark and with prolonged storage the shell may erode quite extensively. Baird (1950) showed that the wounds caused by plugging were almost invariably infected with a gram-negative rod bacterium. He also showed that injections of this bacterium were lethal to lobsters. This suggests that plugging may cause some mortality in storage. It also seemed possible that the wounds may be sites of infection for *Gaffkya homari*, a gram-positive micrococcus, the causative agent of lobster blood disease (Snieszko and Taylor, 1947). European lobster dealers contend that plugged lobsters lose their claws more frequently than banded lobsters. Banding, however, is a relatively slow operation and this is possibly the Canadian fishermen's chief objection. In addition, Canadian dealers contend that bands slip off during storage. Templeman (1948) felt that cutting the extensor tendons showed promise but considered that further study was required.

To obtain further information on the effects of plugging, banding and tendon-cutting during long-term storage two experiments were conducted.

¹Received for publication November 28, 1960.

MATERIALS AND METHODS

For the *first experiment*, 211 unplugged, live, 2-clawed lobsters were obtained on March 24, 1958, by special arrangement direct from the fishermen at Port Maitland, Yarmouth County, Nova Scotia. They averaged 1.2 lb (0.54 kg) in weight and ranged in carapace length from $3\frac{1}{8}$ to $4\frac{1}{2}$ inches (80 to 114 mm). The lobsters were shipped the next day in dry wood shavings to St. Andrews, New Brunswick. During shipment both claws of each lobster were banded with light rubber bands. On arrival on March 25, the lobsters were found to be in excellent condition with only one weak and one dead.

On March 27, the 200 lobsters that remained in excellent condition were divided into 4 lots of 50. One lot was plugged, another banded, and the tendons of the third were cut. The fourth lot was untreated and served as a control. Each lobster was measured and tagged with a serially numbered, metal and rubber carapace tag (Wilder, 1954) before treatment. Each lot was placed in a square tank 3×3 ft (92×92 cm), filled to a depth of 12 inches (30 cm), and supplied with enough running sea water and compressed air to maintain the dissolved oxygen near the saturation level. This degree of crowding, about 1 lb per imperial gallon (1 kg per 10 litres), is well within the limits of commercial practice. At the time of treatment, 3 of the lobsters in each lot were one-clawed.

The plugs were machine-made of basswood, $1\frac{1}{2}$ inches long, $\frac{1}{4}$ inch wide (38×6.4 mm), and $\frac{3}{16}$ inch (4.8 mm) thick at one end, tapering to a point at the other. The upper surface was smoothly rounded, the lower surface flat. Both claws of each lobster in a lot of 50 were plugged by inserting a plug under the shell of the claw in such a manner that the blunt end of the plug protruded at the thumb joint and so inactivated the claw.

The rubber bands were 1 inch long, $\frac{1}{2}$ inch wide and about $1/25$ th of an inch thick ($25 \times 13 \times 1$ mm). These were difficult to stretch with the fingers of one hand and it was most convenient for one person to hold the lobsters, while another applied the bands. The bands were placed around the widest part of the claw near the base of the thumb (Fig. 1).

The extensor tendons of both claws in a lot of 50 were cut carefully with the point of a sharp scalpel as described by Templeman (1948).

The four tanks were checked daily, the temperature recorded and any dead lobsters removed. These were examined and the extent of their injuries recorded. Loss of bands or plugs was also noted. At approximately weekly intervals all lobsters were removed from each tank and examined individually. At about 3-week intervals the lobsters were fed salted herring. This experiment ran for $4\frac{1}{2}$ months, ending August 8, 1958.

The *second experiment* was conducted to determine whether plugged lobsters were more susceptible to infection with *Gaffkya homari* than banded lobsters. On August 18, 1960, during an epidemic of blood disease in southwestern Nova Scotia and in Charlotte County, New Brunswick, 140 recently-caught, unplugged



FIG. 1. Condition of rubber bands when applied (left) and after use for 8 months (right).

lobsters were obtained from the central Northumberland Strait area. They averaged 0.73 lb (0.33 kg) in weight and ranged in carapace length from $2\frac{1}{2}$ to $3\frac{3}{16}$ inches (64 to 81 mm). At the time, there was no evidence of a blood disease epidemic in Northumberland Strait and no unusual commercial mortalities have since been reported there. Blood smears were, however, prepared on August 22 from 59 other lobsters received in the same shipment from the same area. When examined, 40 were vigorous, 10 weak and 9 dead. One vigorous, 2 weak and 1 dead were very lightly infected with *Gaffkya*. The low incidence and lightness of the infection suggest that the lobsters became infected after they reached St. Andrews. The 40 vigorous lobsters were stored in a separate tank of running sea water throughout the experiment.

On August 18, both claws of half the lobsters were plugged with hand-made white pine plugs, $1\frac{3}{8}$ inches long and $\frac{1}{4}$ inch wide (35×6.4 mm). Both claws of the remainder were banded with narrow rubber bands, $\frac{7}{8}$ inch long, $\frac{1}{8}$ inch wide and $\frac{1}{25}$ inch thick ($22 \times 3 \times 1$ mm), considered strong enough to inactivate the claws of these small lobsters. The 140 lobsters were placed in a cylindrical fibreglass tank, 6 ft inside diameter and 3 ft high (183×91 cm) filled to a depth of $2\frac{1}{2}$ ft (76 cm) with running sea water. The experiment proper was started on

August 22 when 2 dead lobsters heavily infected with *Gaffkya homari* were placed in the tank for the lobsters to feed on. At this stage 69 plugged and 67 banded lobsters were alive and vigorous. Additional dead infected lobsters were suspended in the tank in a mesh bag on August 23, 25 and 31. Apart from the 2 dead lobsters placed in the tank on August 22, the lobsters were not fed during the course of the experiment, which was continued until October 11. The tank was checked daily, the temperature recorded and the dead lobsters removed. Several of these dead lobsters were so badly mutilated they were discarded without further study. Blood smears prepared from the remainder were stained with Gram's stain and examined under oil immersion for the presence of *Gaffkya*.

RESULTS

FIRST EXPERIMENT

The weekly mortalities among the plugged, banded, tendon-cut and untreated lobsters are listed in Table I. The percentage accumulative mortalities are plotted in Fig. 2. Total mortalities over the 4½-month period were as follows: plugged 54%, banded 56%, cut tendons 78% and untreated 98%. Moulting was not a factor in these deaths.

TABLE I. Weekly mortalities in lots of 50 lobsters with both claws plugged, banded, tendons cut and untreated.

Week ending		Av. water temp.	Plugged	Banded	Tendons cut	Untreated
		°C				
April	3	4.2	0	0	2	4
	10	4.2	1	2	3	2
	17	4.9	2	0	1	2
	24	7.1	2	2	2	2
May	1	7.2	3	2	1	1
	8	6.8	3	2	3	5
	15	7.3	2	2	1	8
	22	8.2	0	1	2	5
	29	9.1	0	2	0	0
June	5	9.5	0	0	2	0
	12	10.2	1	0	0	6
	19	9.8	0	1	1	1
	26	10.2	2	0	3	7
July	3	11.7	0	1	3	1
	10	12.6	0	1	3	1
	17	12.8	1	2	5	1
	24	13.6	2	4	5	1
	31	13.4	5	5	1	2
Aug.	7	14.0	3	1	1	0
Totals			27	28	39	49

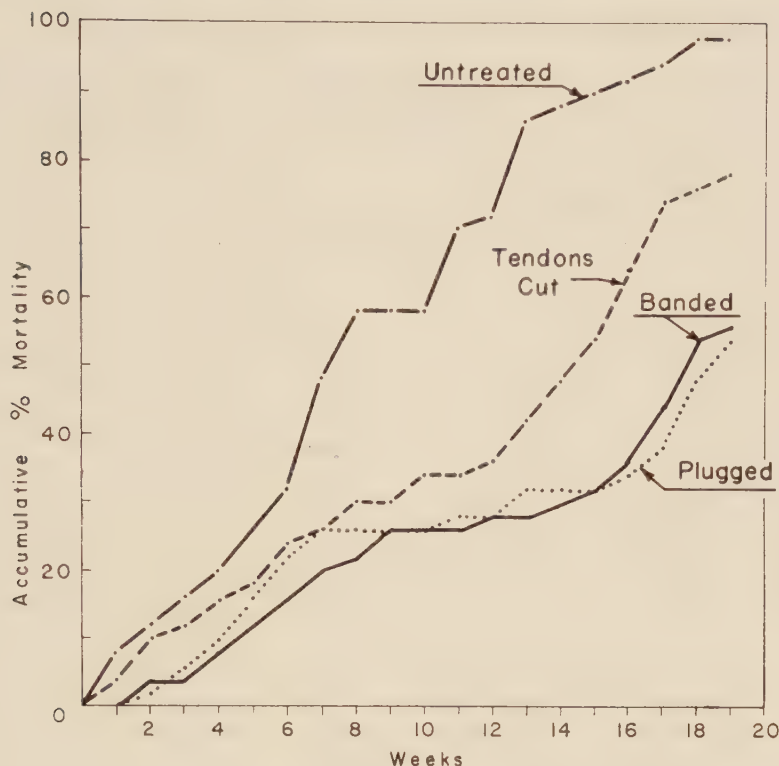


FIG. 2. Accumulative weekly percentage mortalities in lots of 50 lobsters with both claws plugged, banded, tendons cut and untreated.

The tendon-cut lobsters bled quite freely in air for almost a minute. The loss of blood, measured for 7 lobsters averaged 15 cc. No bleeding was evident among the plugged lobsters.

The untreated lobsters lost 12 claws during the course of the experiment, the plugged lobsters 2 claws, the banded and tendon-cut lobsters none.

Only one of the $\frac{1}{2}$ -inch wide rubber bands came off and only 2 plugs came out during the $4\frac{1}{2}$ -month period.

After the close of the experiment proper, the survivors were held alive but given less detailed attention. From August 8 to 13, on September 30 and on November 7th, 8, 4 and 2 of the plugged lobsters respectively were boiled. Most showed a blackening of the shell, meat and extensor tendon in the vicinity of the plug. Several showed quite severe erosion of the shell near the point of insertion of the plug. It was noted that the blackened meat of the two examined on November 7 was definitely off-flavour.

By December 2, 1958, after 8 months' storage, both the rubber bands (Fig. 1) and the wooden plugs had deteriorated appreciably.

SECOND EXPERIMENT

The daily mortalities among the plugged and banded lobsters exposed to *Gaffkya homari*, the numbers examined and the numbers found to be infected are listed in Table II. Percentage accumulative mortalities to October 11 are

TABLE II. Numbers of plugged and banded lobsters dead and infected each day after exposure to *Gaffkya homari*.

Date	Temperature	69 Plugged			67 Banded		
		Dead	Examined	Infected	Dead	Examined	Infected
	°C	no.	no.	no.	no.	no.	no.
Aug. 22	14.5	0	0	0	0	0	0
23	14.4	0	0	0	0	0	0
24	14.1	3	3	3	0	0	0
25	14.1	14	14	14	2	2	2
26	14.0	10	10	9	2	2	2
27	14.4	4	1	1	1	1	1
28	14.8	6	6	6	4	3	3
29	14.5	4	2	2	2	1	1
30	14.6	3	1	1	2	2	1
31	14.5	5	4	4	3	3	3
Sept. 1	14.8	1	1	1	6	3	3
2	14.3	3	2	1	2	2	1
3	14.0	2	2	2	1	1	0
4	14.0	1	1	1	4	3	3
5	13.8	4	4	4	2	2	2
6	13.3	2	1	1	4	4	4
7	13.8	1	1	1	2	2	2
8	13.5	0	0	0	2	2	2
9	14.0	0	0	0	2	2	2
11	14.0	0	0	0	1	1	1
12	14.0	0	0	0	2	2	2
13	14.5	0	0	0	1	1	0
16	14.9	0	0	0	2	2	2
18	14.6	1	0	0	0	0	0
19	13.8	0	0	0	1	1	1
22	14.0	0	0	0	1	1	1
Oct. 3	13.1	0	0	0	2	2	2
7	12.5	0	0	0	1	1	1
Totals to Oct. 11		64	53	51	52	46	42

plotted in Fig. 3. A photomicrograph of a typical blood smear from an infected lobster is shown in Fig. 4. It is obvious that the plugged lobsters died faster and suffered higher mortalities (93%) than the banded (78%). Moulting was not a serious factor in these deaths as only one banded lobster moulted during the experiment. Appreciably lower mortalities occurred among the 40 vigorous lobsters from the same shipment that were not exposed to *Gaffkya* during storage. Only 14 (35%) of these lobsters were dead by October 11, a mortality rate similar

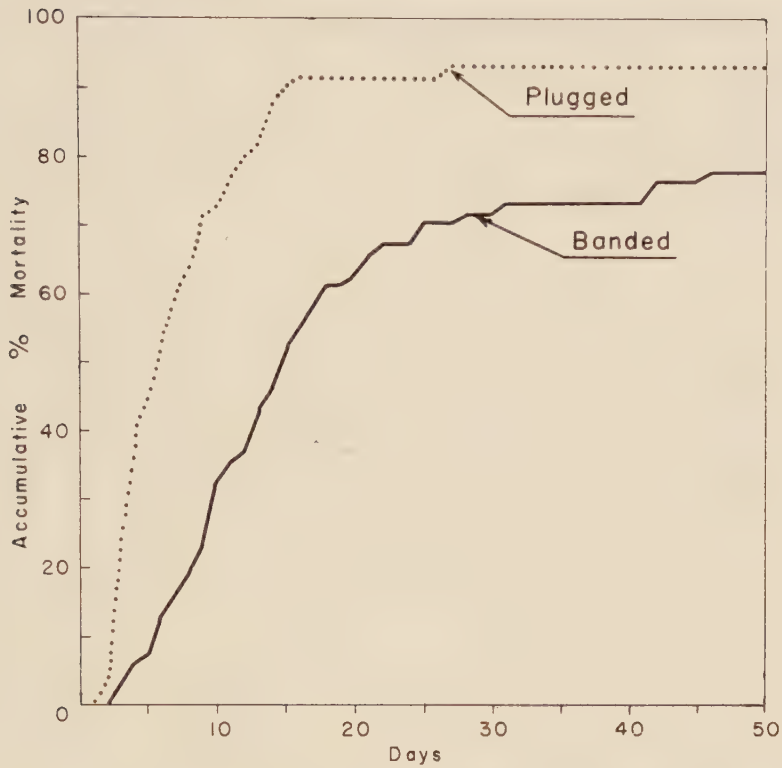


FIG. 3. Accumulative daily percentage mortalities among plugged (69) and banded (67) lobsters when exposed to *Gaffkya homari*.

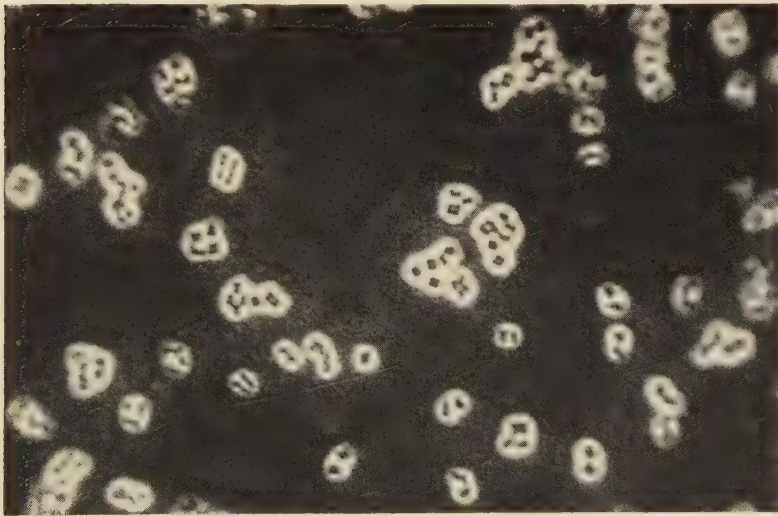


FIG. 4. Typical blood smear from lobsters infected with *Gaffkya homari*. Magnification 890 $\times$. Photomicrograph by P. W. G. McMullon.

to that which occurred in the first experiment conducted at considerably lower temperatures. Of the dead plugged lobsters examined for *Gaffkya*, 96% were found to be infected; of the banded, 91%.

The narrow bands used on the smaller lobsters in this experiment were not strong enough to inactivate all the claws completely. During the experiment these bands were lost and replaced quite frequently.

DISCUSSION AND CONCLUSIONS

It is clear that to reduce mortalities among impounded lobsters some method of inactivating the claws is necessary. Where blood disease is not a factor, banding and plugging are equally effective in reducing mortalities and both methods are superior to tendon cutting. The tendon-cut lobsters did not appear to be adversely affected by the operation and no sudden, heavy mortalities occurred. It seems unlikely, therefore, that the loss of blood which accompanied the tendon cutting contributed appreciably to the higher mortality in this group. At times, particularly during handling, the claws of these lobsters opened when they came in contact with others. Injuries inflicted at such times undoubtedly caused some mortality.

No appreciable loss of claws resulted from any of the three treatments. Apparently this is not a serious problem if the lobsters are handled carefully. Loss of plugs or suitable bands is not serious over a 4½-month period if they are properly applied. The narrow bands used in the second experiment are not suitable for commercial use.

A serious disadvantage of the wooden or plastic plugs is the damage they do to the claws. Not only is the appearance of the shell and meat adversely affected but some meat is destroyed and off flavours develop. Since mortalities among the plugged and banded lobsters in the first experiment did not differ appreciably, there is no reason to believe that a rod bacterium associated with plugging (Baird, 1950) caused appreciable losses in this experiment. There is, however, good evidence that plugged lobsters are more susceptible than banded ones to infection with *Gaffkya homari*, the causative organism of lobster blood disease. For these reasons, the use of plugs to inactivate lobster claws is not recommended.

The advantages of banding the claws with rubber bands seem to outweigh the disadvantages. Although bands are now slow to apply, it seems probable that simple efficient techniques for applying them can be developed. One new technique has recently been described by Taylor (1960).

ACKNOWLEDGMENTS

Most of the observations during the course of these experiments were made by R. C. Murray, Nora M. Young, Patricia A. Holt and D. E. Graham.

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Dietary Marine Fish Oils and Cholesterol Metabolism

3. The Comparative Hypocholesterolemic Activities of Fish Oil and Vitamin A¹

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ABSTRACT

Certain fish liver oils, when present in the diet, prevented hypercholesterolemia in chicks produced by cholesterol feeding. The hypocholesterolemic activity of the oils was proportional to the amount incorporated into the diet. Vitamin A-enriched corn oil produced similar results but corn oil itself was without effect. It was concluded that vitamin A was responsible for 73 to 85% of the activity of the fish liver oil. The cause of the additional activity of the marine oils is at present unknown.

INTRODUCTION

PREVIOUS WORK in this laboratory indicated that the hypocholesterolemia induced in chicks by cholesterol feeding was prevented by dietary fish oils such as lingcod liver oil and halibut liver oil (Wood and Biely, 1960a). The hypocholesterolemic factor was located in the unsaponifiable portion of the oil (Wood and Biely, 1960b) and its identity tentatively suggested as Vitamin A (Wood, 1960). However, the evidence for this postulation was unsatisfactory in some respects. For instance, when crystalline vitamin A acetate was incorporated into the cholesterol-containing diet in place of fish liver oil, its hypocholesterolemic activity was not so great as might be expected. Moreover, the correlation between activity and amount of dietary vitamin A was rather indefinite. The present studies were therefore undertaken to elucidate whether vitamin A was indeed the active agent in the fish liver oils.

MATERIALS AND METHODS

BIRDS

Day-old white leghorn cockerels were placed for one week on the control diet. At this point birds whose body weights deviated widely from the average were discarded and the remainder distributed in groups of sixteen per cage. The groups were then placed on the appropriate test diets for 14 days.

¹Received for publication February 8, 1961.

DIETS

The control diet was formulated as shown in Table I. Additions to this diet listed in the accompanying Tables and Figures were substituted isocalorically for the sucrose. The diets were stored at 2°C and sufficient food for one day

TABLE I. Composition of the control diet. The caloric value of the diet = 3.6 calories/g.

	%		%
Ground wheat	41.20	Distillers' solubles	1.87
Cornmeal	7.50	Dehydrated grass	0.94
Ground oats	3.75	Iodized salt (fine)	0.37
Middlings	3.75	Ground limestone	0.75
Bran	3.75	Manganese sulphate	0.01
Soybean meal	5.62	2250 A, 300 D, vitamin oil	0.20
Fishmeal	1.50	Nicarbazin	0.04
Meatmeal	3.75	Sucrose	25.00
Riboflavin 50 mg/100 lb feed			

only was placed in the feed troughs. The amount supplied to the chicks was adjusted so that the calorie intake was the same on all diets. The average food intake during the fourteen-day test period varied from 13 to 15 g/chick/day depending on the diet.

DETERMINATION OF SERUM CHOLESTEROL

The birds were starved for 18 hours prior to the collection of the blood from the brachial vein. Samples from four birds were pooled and the serum collected in the normal manner. The total cholesterol concentration in the serum was determined using the method of Sperry and Webb (1950).

RESULTS

The experimental cockerels were distributed into six groups. One group was fed the control diet, a second group the control diet + 1% cholesterol, and the remaining four groups the control diet + 1% cholesterol + respectively 1, 2, 3 and 4% lingcod liver oil with a potency of 42,500 I.U. vitamin A/g. The serum cholesterol levels of the chicks on the various diets are shown in Fig. 1. The broken line indicates the cholesterol concentration in chicks fed the control diet. The presence of 1% cholesterol in the diet increased the mean serum cholesterol concentration from 194 mg/100 ml to 686 mg/100 ml. This increase was prevented by the dietary fish liver oil, the hypocholesterolemic effect being proportional to the amount of oil incorporated into the diet. The presence of 4% oil prevented almost completely the increase in serum cholesterol.

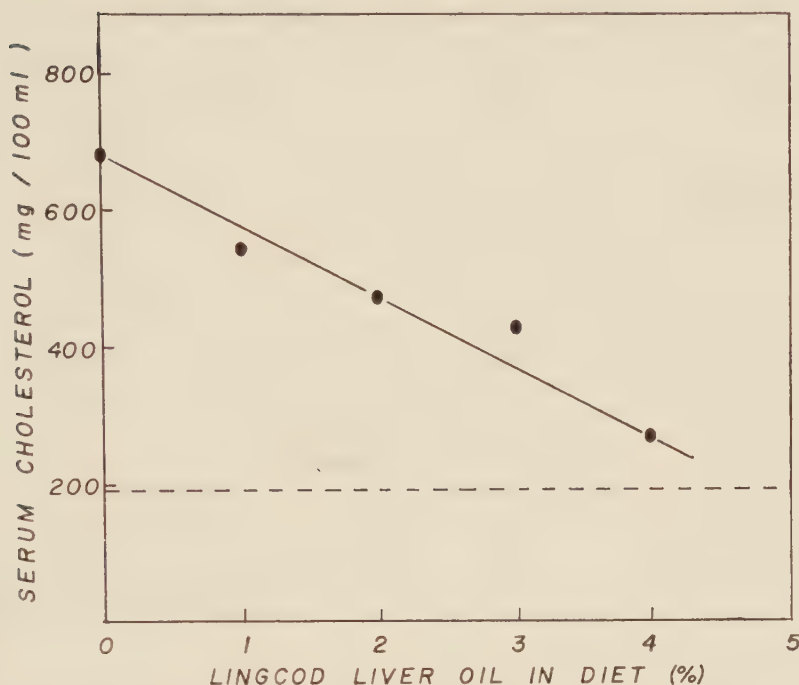


FIG. 1. The prevention of hypercholesterolemia in cholesterol-fed chicks by different amounts of dietary lingcod liver oil.

A similar experiment was carried out using a vitamin A-enriched corn oil instead of the lingcod liver oil. The enriched oil was prepared by dissolving crystalline vitamin A acetate in corn oil until the potency was 42,500 I.U. vitamin A/g oil. The results obtained with the enriched corn oil (Fig. 2) were similar to those obtained with the fish oil. The hypocholesterolemic properties of the diets increased with the concentration of the oil so that a 4% level in the diet was sufficient to afford almost complete protection against the effect of the dietary cholesterol.

Two different samples of lingcod liver oil varying greatly in their vitamin A content were tested for hypocholesterolemic activity. The oils were incorporated into cholesterol-containing diets in different amounts but the total quantity of vitamin A added was the same in both cases. The effects of the diets on serum cholesterol levels are shown in Table II. The hypocholesterolemic action of the fish oil-containing diets appeared to depend on the vitamin A content rather than on the amount of oil in the diet. The incorporation of corn oil into the diets at the 4 and 9% levels was without effect on serum cholesterol concentration.

The above experiments, although demonstrating the similar effects of fish oils and vitamin A-enriched corn oil, did not yield a direct comparison of the oils because the experiments were carried out independently. To clarify this

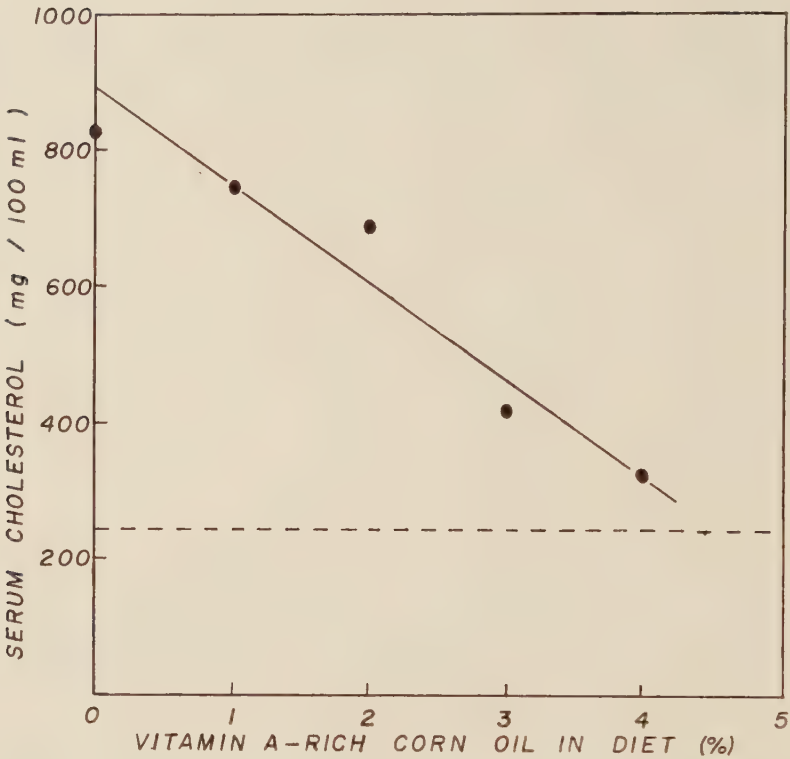


FIG. 2. The prevention of hypercholesterolemia in cholesterol-fed chicks by different amounts of dietary vitamin A-enriched corn oil.

TABLE II. Comparative effect of the same total amount of vitamin A from two different lingcod liver oils on serum cholesterol levels in cholesterol-fed chicks.

Addition to cholesterol-containing diet ²	Vitamin A potency (I.U./g oil)	Mean serum cholesterol (mg/100 ml)
None	—	990 ± 68
4% corn oil	—	980 ± 88
9% corn oil	—	948 ± 146
4% lingcod liver oil	42,500	176 ± 34
9% lingcod liver oil	18,900	179 ± 23

²Cholesterol-containing diet was the control diet + 1% cholesterol.

point, vitamin A-enriched corn oil was compared directly with various fish oils (Table III). In every instance the enriched corn oil was less effective in preventing hypercholesterolemia than was the fish liver oil with a comparable vitamin A content. Statistical analysis showed that the difference was significant

TABLE III. Comparative effect of fish liver oils and vitamin A-enriched corn oil on serum cholesterol levels in cholesterol-fed chicks.

Expt. no.	Number of birds per diet	Addition to cholesterol-containing diet ²	Vitamin A potency (I.U./g oil)	Mean serum cholesterol (mg/100 ml)	Relative calorie intake	Relative weight gain	Relative hypocholesterolemic activity ³
1	16	10% dogfish liver oil	8,300	435 ± 86	100	100	138
	16	10% corn oil	8,300	618 ± 156	105	131	100
2	64	10% dogfish liver oil	7,300	306 ± 95	100	100	-
	64	10% corn oil	7,300	483 ± 133	98	136	-
3	16	4% lingcod liver oil	42,500	214 ± 33	100	100	119
	16	4% corn oil	42,500	312 ± 133	106	120	100
4	16	9% lingcod liver oil	18,900	179 ± 23	100	100	118
	16	9% corn oil	18,900	301 ± 114	103	114	100

²See footnote to Table II.

³Hypocholesterolemic activity is designated; mean serum cholesterol level for birds on cholesterol-containing diet minus mean serum cholesterol level for birds on the same diet plus the oil. The relative activities were calculated taking the enriched corn oil diet as 100.

at the 1% level. Although the calorie intakes of the chicks on the two diets were similar, the weight gains of the chicks were always greater on the enriched corn oil diets. Moreover, there appeared to be an inverse relation between the weight gain of the chicks and the hypocholesterolemic activity of the oil supplements.

DISCUSSION

The results presented here show that the hypocholesterolemic effect of fish liver oils can be duplicated by vitamin A-enriched corn oil, although corn oil itself is without effect. It has also been shown that the amount of vitamin A incorporated into the diet is more important from the view of preventing hypercholesterolemia than is the amount of fish oil itself. Moreover, since corn oil has no effect on serum cholesterol levels, the observed hypocholesterolemic effects of different amounts of vitamin A-enriched corn oil must be due to the vitamin A content. In other words, the degree of prevention of hypercholesterolemia is proportional to the vitamin A content of the diet. The rather indefinite relation observed previously (Wood, 1960) was due probably to the fact that at that time the vitamin A was added in the dry state and a less homogenous diet with respect to the vitamin was therefore obtained. Although the results discussed above indicate that vitamin A is the major hypocholesterolemic agent in fish liver oils, only 73 to 85% of the activity of the oils can be attributed to their vitamin A content (calculated from the relative hypocholesterolemic activities in Table III). The reason for the additional activity is at present unknown.

It is interesting to note the inverse proportionality between the hypocholesterolemic action of the diets and the weight gain of the chicks. Since the calorie intake was similar on the different diets, the fish oil may therefore exert its "extra" effect by lowering the absorption of food including the cholesterol. On the other hand, the additional activity may be due to another hypocholesterolemic agent in the fish oil, to the presence in the oil of a substance which increases the action of vitamin A, or perhaps to a form of vitamin A in the fish oil which is more active than the acetate form used to fortify the corn oil. Further investigations are being carried out to determine the reason for the additional activity of the fish oils.

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Radioactive Iron as a Fish Mark¹

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ABSTRACT

Experiments designed to test the feasibility of using radioactive iron as a fish mark are described. The biological half-life (turnover) of iron in speckled trout (*Salvelinus fontinalis*) was found to be probably at least 2 years. Iron-59, with a physical half-life of 45.1 days, was used in the experiments.

INTRODUCTION

MUCH INVESTIGATION of the contamination of fish with radioisotopes has been done, in particular, by Japanese workers. The source of this contamination has been fallout from nuclear explosions mainly, but some has come from effluents from nuclear reactors. The use of radioisotopes as fish marks has, however, received little investigation, probably because of difficulties in obtaining the necessary materials. Two recent Russian investigations should be mentioned. Bogoiavlenskaia (1959) investigated the use of calcium-45 as a mark for fish. The mark obtained appeared to have a useful life of approximately one year, using their counting technique. It should be noted that Ca-45 concentrated almost entirely in the bony structures of the fish, such as gill covers, scales and axial skeleton. Calcium-45 emits a single relatively soft beta ray with no associated gamma emission. Reading the live fish, therefore, could be extremely difficult as the sample count approached the same level as background. The physical half-life of Ca-45 is 164 days; this is sufficiently long for most experiments. Karzinkin, Soldatova and Shekhanova (1959) marked 106,000 young sturgeon with phosphorus-32 by feeding them oligochaetes (*Enchytraeus albidus*) which had been fed on either a flour suspension or hydrolyzed yeast containing the radioisotope. These authors found that the mark remained useful for 2.5-3.0 months, using their counting technique. Phosphorus-32 has only a 14.3 day half-life and would not normally be useful for a long-term experiment.

Of the 775 radioisotopes of elements 1-92 inclusive, listed by Bradford (1957), very few can satisfy these criteria. All alpha ray emitters must be

¹Received for publication November 9, 1960.

eliminated because of the biological potency of these particles; the majority of the remainder are eliminated because of too short a physical half-life or biological incompatability, such as chemical toxicity, energetic radiation and organ concentration.

Of the potentially useful radioisotopes, radioactive iron appears to be the most likely to be useful. Two radioisotopes exist; iron-55 has a physical half-life of 2.94 years and decays by electron capture, the only emission being the characteristic X-ray of the daughter manganese-55. Iron-59 has a physical half-life of 45.1 days and decays by negatron emission with emission of three different gamma rays from the daughter cobalt-59 nucleus (Overman and Clark, 1960, pp. 7-10). Iron-59 was chosen for the work to be described, since the background level in our laboratory is quite high; distinction between background count and the gamma rays of Fe-59 is immensely simpler than separating the X-ray associated with decay of Fe-55. However, since the radioisotopes are chemically identical, results obtained are applicable to both.

MATERIALS AND METHODS

High purity Fe-59 was obtained for the experiments from the Oak Ridge National Laboratory, Oak Ridge, Tenn. Table I shows the specifications of the material.

TABLE 1. Specifications of Fe-59 solution obtained from Oak Ridge National Laboratory. Data given are for the original 1-millicurie (mc) shipment; subsequent shipments varied somewhat in specific activity, concentration, and Fe-55 and Co-60 content.

Chemical form:	FeCl ₃ in HCl solution
Acidity:	1.98 N
Concentration:	3.98 $\pm$ 5% mc/ml
Specific activity	8378 mc per gram of iron
Concentration Fe-55:	0.064 mc/ml
Concentration Co-60:	—0.0018 mc/ml
Total Fe per mc:	0.1425 mg

On receipt, the solution was diluted to a concentration of 5 microcuries per millilitre (μ c/ml) with a highly acid (pH 2.25) solution of acriflavine hydrochloride. The acriflavine was found to be necessary to prevent infection in the fish when the solution was injected into the body cavity. Ferric chloride is hydrolyzed to the hydroxide in all but highly acid solutions; ferric hydroxide is not soluble in water of normal pH range, and thus the highly acid solution was necessary to maintain the radioisotope in solution. The fish apparently did not suffer

from the effects of the injection. The injections were made through the ventral body wall just anterior of the ventral fins. Great care was taken to avoid puncturing any of the organs. It was found that 10-cm trout could be injected with the solution at the rate of 5 per minute; accuracy was achieved by the use of 1-ml tuberculin syringes with No. 25 needles. No anaesthetic was necessary.

Two methods of radio-assay of the specimens were used. In Method 1, the tip of a Nuclear-Chicago Corporation DS8-1 6-mm needle scintillation probe was placed over the heart-liver region of the fish's belly and the counts made with a portable ratemeter. In Method 2, the fish were kept in an annular tank with the detector (a special gamma-ray-sensitive Geiger-Muller tube) at the centre so that the fish were always in the same geometrical relationship to the probe. Counts were registered by a laboratory ratemeter, and recorded on a strip-chart recorder continuously. Provided that a radioisotope emitting hard gamma rays is being used, the second method is much superior to the first, since the fish are not handled. However, where a yes or no answer is required, or where error due to variations in geometry between fish and detector can be tolerated, the first method enables many more fish to be handled. It is also the field method of choice. Figures 1 and 2 show the apparatus for radio-assays by each method.



FIG. 1. Radio-assay of Group I trout, using needle scintillation probe.



FIG. 2. Constant-geometry tank for radio-assay of Group II trout.

The loss of an element in a biological system, that is, turnover, follows the exponential decay law. Thus, the effective half-life of a radioisotope in a fish is the combined product of the physical decay and the biological loss. The relationship between effective half-life (T_e), physical half-life (T_P), and biological half-life (T_B) is:

$$\frac{1}{T_e} = \frac{1}{T_P} + \frac{1}{T_B} \quad (1)$$

The effective half-life of the isotope in the experimental fish was obtained by calculating the slope (b) and the Y-axis intercept ($\log N_0$) of the least-squares line relating the logarithm of the count rate ($\log N_t$) to time (t), for each fish assayed (cf. Fig. 3, which however shows geometric mean values for each day):

$$\log N_t = \log N_0 - bt$$

Half-life (T_e) was then calculated from the slope using the expression:

$$T_e = \frac{\log 2}{b} = \frac{0.3010}{b} \quad (3)$$

RESULTS

GROUP I

Twenty-five *Salvelinus fontinalis* were injected with 1 ml of Fe-59 solution, containing $1.0 \mu\text{c}$ of Fe-59, on July 4, 1960. The total ferric chloride concentration was 0.576×10^{-9} g/ml. The trout were kept in a wire cage floating in running water at 10°C . Radio-assays of the individual fish were started on July 5 by Method 1 and continued until October 3, when a failure occurred in the

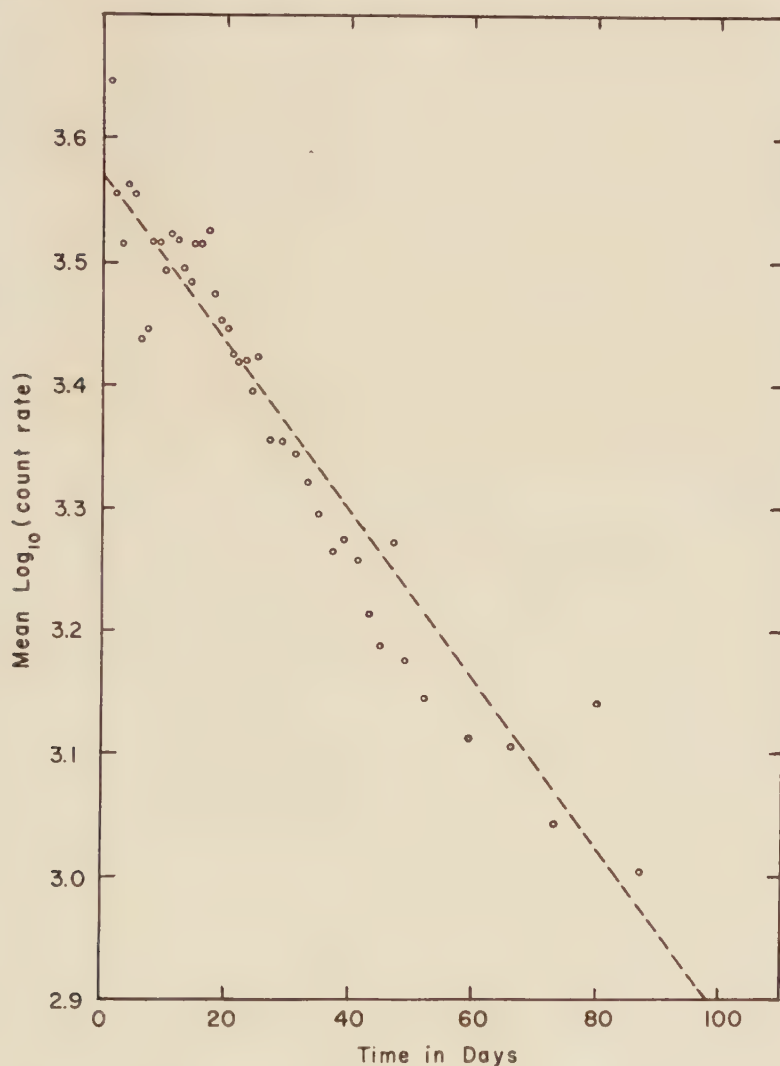


FIG. 3. Relationship between $\log_{10}(\text{count rate})$ and time for Group I trout, from radio-assay by the needle scintillation probe over the heart-liver region. Values plotted are geometric means for all fish assayed on each day.

laboratory's dechlorinating system and all specimens died. Eight of the specimens had died from handling and partial chlorine intoxication prior to this date. The relationship between count rate and time (Fig. 3) has a slope of -0.006893 log units per day (Table II), and the corresponding effective half-life is, from (3), 43.7 days. From (1), the biological half-life is estimated as approximately

TABLE II. Analysis of radio-assay data for trout of Group I and Group II.

Statistic	Symbol	Group I	Group II
Number of individual radio-assays	n	823	515
Average time of assay, days	t	25.6	3.447
Average of logarithms of counts per minute	$\log N_t$	3.393	2.6882
Regression coefficient (slope)	b	-0.006893	-0.006984
Standard error of b	...	0.000530	0.000391
Correlation coefficient	r	-0.413	-0.714
Probability of significance	P	-0.01	-0.01
Y-axis intercept	$\log N_0$	3.569	2.7123
Effective half-life, days	T_e	43.7	43.1
Physical half-life, days	T_p	45.1	45.1
Biological half-life, days	T_B	1408	978
95% confidence limits of T_B , days	...	241, ∞	332, ∞

1408 days. There was no evidence during the experiment that the radioisotope had any effect on the trout; deaths from handling and chlorine in other tanks were as numerous.

Considerable day-to-day variation occurred in the counts of this group. Minor changes in geometrical relationship of detector and source, i.e. error in probe placement, caused much of this, and there was also the effect of the fish's struggles during the readings. There was an apparent engorgement of the heart-liver region as a result of these struggles, since a passive fish showed a lower count than if it were struggling. However, most of these variations averaged out, and had little effect on the slope of the regression line. Also, despite equal amounts of radioisotope injected into each fish, there was much individual variation. Differences in size resulted in differing dilutions of the isotope, and also resulted in different geometrical relationships with the detector. The 5% confidence limits on the estimate of biological half-life are 241 days to infinity.

GROUP II

The effect of handling the trout in Group I daily for the first month and less frequently afterwards might have had some effect on the turnover of iron. In order to check this possibility, a group of 6 trout, approximately 17 cm long, were marked with $10\text{-}\mu\text{c}$ each of Fe-59 and were placed in the annular tank mentioned previously. Continuous recordings of the radioactivity level of these fish were made, and the data taken from the strip chart. The regression analysis

(Table II) yielded an effective half-life of 43.1 days and thus a biological half-life of 978 days. The 5% confidence limits on the latter place the biological half-life between 332 days and infinity. It should be noted that the dosage of 10 μ c was apparently too much, in that 2 trout died on the 30th day and the remaining 4 on the 32nd day after injection.

DISCUSSION

In order that a radioisotope may be useful as a fish mark in the field, three criteria must be satisfied. These are:

1. the element must have a slower turnover rate in the fish, i.e., a long biological half-life in relation to the fish's longevity;
2. a radioisotope of the element must exist whose physical half-life is reasonably long in relation to the fish's longevity;
3. the radioisotope must emit radiation which is reasonably detectable with field equipment, but at the same time, with a low enough energy transfer to the fish so that little or no biological damage is done.

By using iron-59, it has been shown that iron has a very long biological half-life in trout, i.e., a slow turnover rate. Iron-59 has a rather short physical half-life of 45.1 days, but another radioisotope of iron, Fe-55, has a half-life of 2.94 years. Iron-55 does have the disadvantage of a very weak emission, the 5.9-kilovolt characteristic X-ray of the daughter Mn-55. Detection of this X-ray entails the use of an X-ray spectrometer; with the advent of transistorized instruments, this requirement presents no particular difficulty. Assuming therefore that Fe-55 is used, a life-time mark for most species of fish should be possible; it is unlikely that other species of fish would show biological half-lives of iron much different from trout.

Aside from possible detection difficulties, two other points should be mentioned. First, in the present study, the radio-iron was introduced into the fish by injection. Although this is probably the most efficient method in terms of equality of mark and maximum economy of radioisotope, it is only useful where the fish are large enough to be handled. Trout as short as 8.0 cm were successfully injected in trials, but the losses from handling and damage from the needle were prohibitive in smaller fish. Introduction of the radio-iron through the food for smaller fish would probably be successful, although possibly wasteful of the isotope. This method would also result in considerable contamination of the tank and waste water system, since it is likely that the fish would not take up all the available iron. The method used in Bogoiavlenskaia's (1959) experiments, where Ca-45 was absorbed directly from the surrounding water, will not work for iron. Iron salts are quickly hydrolized in water of normal pH range, and most of the material precipitates out.

The second point lies in the fact that fish grow, and hence the specific activity of the radio-iron in the blood goes down even though there may be very slow physical and biological loss. For this reason, long-term marks made by introducing radio-iron into very small fish could be rendered extremely difficult to detect if the fish grow very large.

One possible drawback to the use of Fe-55 as a mark lies in the presence of this radioisotope in nuclear fallout. The probability of interference from fallout radio-iron is small at the present time, but should nuclear testing be resumed, it could have serious consequences.

Another possible complication arising from the use of any radioisotope mark lies in the possibility that some of the radioisotope will be transferred to a predator eating the marked fish. Provided that only interspecific predation occurs, this transfer could be advantageous, in determining the amount of predation. However, intraspecific predation could result in a spread of a mark across several year-classes and thus could obscure results.

For short-term marking Fe-59 is much to be preferred. The characteristic gamma rays of this isotope make it extremely easy to identify with portable gamma spectrometers, and these instruments can detect very low levels of radioisotope by practically eliminating background interference. The only limitations associated with Fe-59 are the increased hazard of biological damage to the specimen, and the relatively short physical half-life. The length of time which a mark will persist will depend entirely on the sensitivity of the detecting equipment, the dilution factor of growth, and the original amount of radioisotope in the fish. The mark never vanishes completely, since the decay is exponential both physically and biologically. Thus, in the long run, the limit in time of usefulness is entirely dependent on the instrumentation.

To summarize, iron turnover in trout is quite slow; a mark using radioactive iron is thus possible for fish over 8 cm long by injecting either Fe-55 or Fe-59. In smaller fish some method of introducing the radioisotope through the food must be employed. With Fe-55, a lifetime mark should be achieved, provided extremely sensitive and selective radio-assay equipment is used. Short-term marks, probably up to a year, could be achieved using Fe-59, detection being by means of a gamma spectrometer.

Possible dangers to humans from consumption of radioisotope-marked fish can exist, depending on the radioisotope used and the amount in each fish. Assuming 1.0 μc of Fe-59 in each fish, and also assuming that the whole fish were eaten by a man with 100% absorption of the iron, it would require 20 fish to equal the maximum permissible body burden for Fe-59, as specified in Handbook 69, National Bureau of Standards (1959), for occupational exposure. Using one-tenth this level (2 μc) for the general public, only 2 fish eaten would supply the maximum permissible body burden. However, most of the Fe-59 in the fish is in the blood, and would largely be removed during cleaning; also absorption of iron from food is not perfect and probably rarely exceeds 10%. Thus, there would be little likelihood of danger to man from the consumption of fish marked

with Fe-59, provided marking levels were low, and a low percentage of the population were marked. For Fe-55, the maximum permissible burden for total body is 3 millicuries; since the marking would still be 1 microcurie per fish, danger to man becomes negligible.

ACKNOWLEDGMENTS

I wish to thank Mr J. Hoy, Fisheries Research Board of Canada Biological Station, London, whose invaluable technical assistance made the work possible.

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Plasma Proteins of Coho Salmon, *Oncorhynchus kisutch*, as Separated by Zone Electrophoresis^{1,2}

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ABSTRACT

Plasma proteins, as separated by zone electrophoresis, of coho salmon have been investigated from an early age to spawning and death. A protein fraction which may be similar to γ -globulin in other vertebrates increased throughout the period studied. Smolt transformation was associated with a temporary disappearance of the fastest migrating protein fraction. A lipoprotein fraction, presumably serum vitellin, was associated with egg formation. Serum vitellin was absent from the plasma of males, immature females, spawning females and spawned-out females.

INTRODUCTION

EGG PRODUCTION in oviparous vertebrates is associated with many changes in the plasma proteins of the female. These protein changes are under hormonal control and can be induced in immature animals of either sex or in castrates by exogenous estrogens. Laskowski (1935) and Roepke and Hughes (1935) demonstrated that sera from laying fowl contained a phosphoprotein, serum vitellin, which was not present in non-laying female or male birds and was absent from mammalian sera. Subsequent investigators have demonstrated the presence of serum vitellin during egg formation or following estrogen administration in pigeons (McDonald and Riddle, 1945), in ducks (Mandel *et al.*, 1947), in reptiles (Laskowski, 1936; Dessauer and Fox, 1959) and in fishes (Laskowski, 1936; Bailey, 1957).

Dr G. S. Ridgway (personal communication, 1959) investigating geographically correlated differences in sockeye salmon found an antigenic serum component in mature or maturing females which was absent from males. This antigenic character was also found in high concentrations in salmon eggs. Similar components have been found in mature female carp sera (Uhlenhuth and Kodama, 1914; quoted by Sasaki, 1932) and have been extensively studied in fowl in which serum vitellin and ovovitellin are serologically related (Roepke and Bushnell, 1936; Hosoda, *et al.*, 1955).

Free and zone electrophoretic analyses of avian serum proteins have shown that egg formation or estrogenization is associated with the appearance of a lipoprotein containing lipid phosphorus but not protein phosphorus (McKinley *et al.*, 1953) and pre-albumin components (Moore, 1948; Brandt *et al.*, 1951; Heim and Schechtman, 1954) in addition to serum vitellin. At the same time there is

¹Received for publication December 22, 1960.

²Paper No. 2 concerning the physiology and behaviour of salmonid fishes, from the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C. Paper No. 1 of this series appeared in the *Canadian Journal of Zoology*, **38**: 199-202, 1960.

a temporary disappearance of α_1 -globulin together with its associated lipid (McKinley *et al.*, 1954; Vanstone *et al.*, 1955).

The plasma proteins of non-avian egg laying vertebrates have not been extensively investigated in relation to sex or physiological state by electrophoretic methods. Dessauer and Fox (1959) demonstrated that two slow moving fractions in plasma of viviparous snakes were mainly responsible for increased plasma protein levels during estrus. These fractions may be similar to the PP zone and fraction 8 of Vanstone *et al.*, (1955) or the P₂ and P₁ fractions of McCully *et al.* (1959) which were identified tentatively as lipovitellin and lipovitellenin complexes. Drilhon (1954 a, b) working with carp obtained results suggesting that maturing females contain greater amounts of albumin and α -globulin than males and that lipids are associated with albumin and β -globulin in maturing females.

A preliminary investigation of the plasma proteins of coho salmon (*Oncorhynchus kisutch*) is the subject of the present report and forms a part of the study of the physiology and behaviour of salmon outlined by Brett (1957). No attempt has been made to present quantitative results since a pure race of fish was not examined and it has been found that the relative amounts of certain protein fractions vary between races of coho salmon (unpublished observations). Similar differences in plasma protein pattern have been demonstrated between races of man (Smithies, 1955), of snakes (Dessauer and Fox, 1958) and of sockeye salmon (Mr I. H. Carlson, personal communication, 1960).

MATERIALS AND METHODS

Yearling presmolting coho and yearling coho smolts were reared from eggs under laboratory conditions. In addition some smolts were captured at the beginning of their seaward migration in the Great Central Lake and Sproat Lake drainage system on the west coast of Vancouver Island. Prepuberal 2-year-old fish were obtained by trolling in Georgia Straits off Nanaimo, and maturing fish were captured at the beginning of their spawning migration or on the spawning grounds of the watershed of Great Central and Sproat Lakes.

Blood samples were obtained from the caudal artery and vein by amputating the tail and collected in heparinized bottles. The whole blood was stored on ice and transported to Nanaimo where the plasma was obtained by centrifugation. All samples were in the electrophoretic apparatus within 6 hours of sampling.

The ages of all sea-going and maturing fish in the early part of their migration were determined by scale readings. Due to scale resorption it was found impractical to obtain scales from spawning fish.

Zone electrophoresis employing aqueous veronal buffer (pH 8.6, ionic strength 0.05) was carried out as described by McKinley *et al.* (1954) except insofar as the papers were supported on a sheet of pebbled Plexiglass (Sehon *et al.*, 1956) and were

completely moistened with buffer before the plasma samples were applied. The proteins were fractionated for 18 hours at a current of 0.5 mA/cm and the developed electropherograms were then dried at room temperature. Proteins on strips cut from the electropherograms were stained with Azocarmine B (Harders and Van Mulken, 1953) without prior extraction with fat solvents. Other strips cut from the same electropherograms were stained for lipid with Oil Red O (Talluto *et al.*, 1958).

RESULTS AND DISCUSSION

Typical electropherograms obtained at different stages during the life cycle of coho salmon are presented in Fig. 1. No sex differences were apparent prior to gonadal development and the protein patterns from laboratory reared and wild yearling fish were similar and will not be discussed separately. Plasma from pre-smolting yearling coho contained 5 protein fractions as separated by the present methods. These fractions, in order of decreasing mobility have been designated 1, 2, 3, 4 and 5. Lipid staining was associated with fraction 2.

Many physiological changes occur concurrently during the smolt transformation (changes preceding and during migration from fresh to salt water—usually after one year in fresh water for coho). These changes have been discussed by Pickford and Atz (1957) and by Baggerman (1960). Carlson (personal communication, 1960) has demonstrated that fraction 1 is absent from smolting sockeye salmon plasma but that it reappears shortly after the fish enter salt water. Carlson's findings were extended to smolting coho salmon in this study.

Plasma electropherograms obtained from prepuberal 2-year-old coho which had spent a year in salt water were qualitatively similar to those obtained from pre-smolting yearlings. However, fraction 5 in all samples examined was more distinct at this stage and may be similar to γ -globulin in other vertebrates. Fraction 5 was the slowest moving component and was less concentrated, relative to the other fractions, in young fish. This increase may be related to increased antibody production as the fish is exposed to various organisms or it may be a normal development as the fish matures. Similar results have been obtained for γ -globulins in mammals (Moore *et al.*, 1945) and in birds (Brandt *et al.*, 1951; Vanstone *et al.*, 1955).

Other than a progressive increase in fraction 5, electropherograms of plasma obtained from maturing, spawning and spawned out 2½-year-old males were similar to those of immature fish of either sex. By contrast, with the onset of maturation in the female, a sixth plasma protein fraction appeared. This sixth fraction, fraction 6, which was also associated with lipid staining material, had the same mobility as fraction 4 and was admixed with it. The resulting mixed fraction was designated "4 + 6" in Fig. 1. Fraction 6 is probably a mixture of the lipovitellin and lipovitellenin complexes reported by McCully *et al.*, (1959)

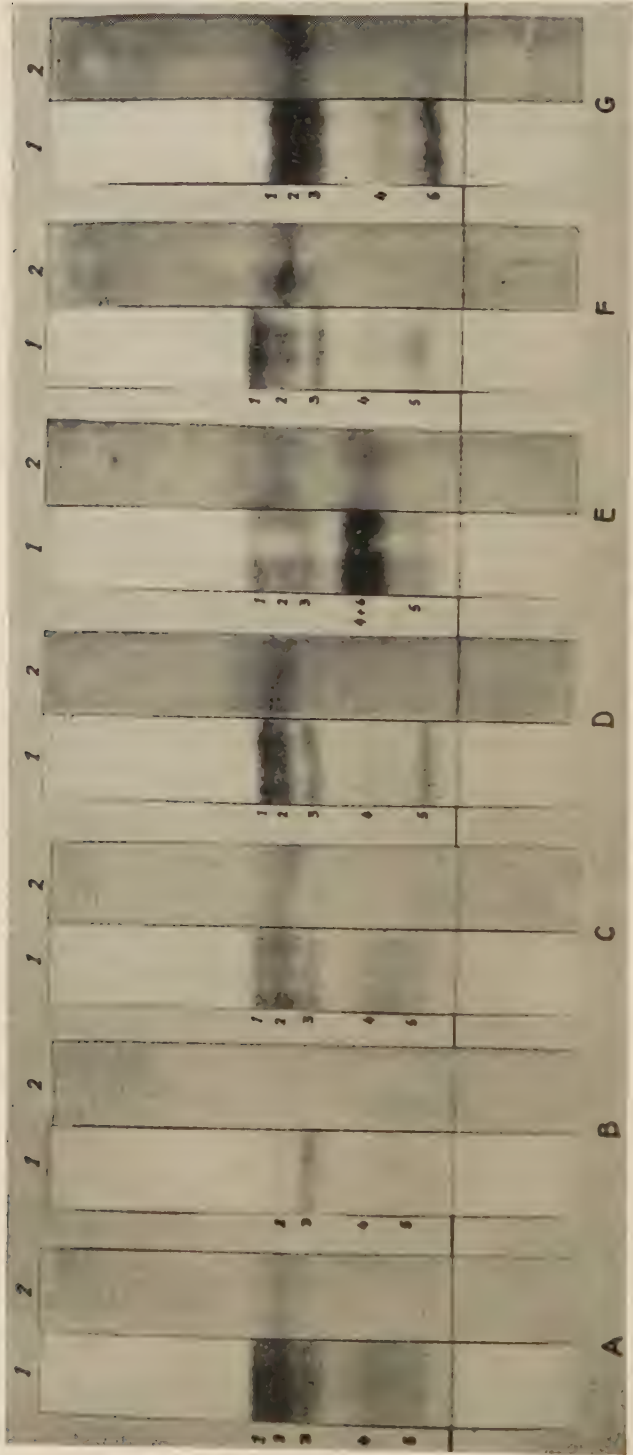


FIG. 1. Separation of plasma protein zones by electrophoresis with veronal buffer, pH 8.6, ionic strength 0.05, on Whatman 3MM paper. Temperature 5°C. Samples applied at pencil line. Status (1) Azocarmine B (protein), (2) Oil Red O (lipid).

A. Pre-smolting yearling coho in fresh water.
B. Smolting yearling coho in fresh water.
C. Prepuberal 2-year-old coho in salt water.
D. Maturing 2½-year-old male coho in fresh water.
E. Maturing 2½ year-old female coho in fresh water.
F. Spawned-out male coho in fresh water.
G. Spawned-out female coho in fresh water.

in transit to the developing ova. This fraction, together with its associated lipid, disappeared from the plasma at about the same time that the eggs were released from the ovarian tissue. It was absent from spawning or spawned-out fish.

Laskowski (1936), working with female trout and tench, reported a similar decrease in serum vitellin coincident with maturation of the eggs. In addition Ridgway (personal communication, 1959) has found an antigenic component in maturing female sockeye sera and in sockeye eggs which was absent from male sera. His results might be explained by the *de novo* appearance of fraction 6 in maturing female plasma. These observations lend support to the theory that fraction 6 is indeed a yolk constituent, or more correctly, a mixture of yolk constituents including serum vitellin. In the bird these yolk components are produced in large part by the liver (Ranney and Chaikoff, 1951; Ranney *et al.*, 1951; Vanstone *et al.*, 1957). A similar site of synthesis may be postulated in the fish. These materials are then transported by the blood to the developing ova. At the completion of yolk development, but prior to spawning, the production of these constituents ceases with a resulting decline in their plasma levels.

ACKNOWLEDGMENTS

The authors wish to thank Mr D. B. Sutherland and Mr D. Pozar for rearing the laboratory fish, Mr C. T. Shoop for invaluable assistance in obtaining all samples of wild fish and Mr T. H. Bilton for the age determinations on wild fish. The authors wish also to thank Dr J. R. Brett for helpful advice and criticism of the manuscript.

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Influence of Size Upon the Adaptation of Steelhead Trout (*Salmo gairdneri*) and Chum Salmon (*Oncorhynchus keta*) to Sea Water^{1,2}

BY ARTHUR H. HOUSTON³

ABSTRACT

Steelhead trout in the smolt phase of development adapted to sea water (salinity 22–24 parts per thousand) more rapidly and with less extensive departures from regulated conditions of water–electrolyte balance than did the larger post-smolts. By contrast, the extent and duration of the corresponding changes accompanying adaptation of juvenile chum salmon to sea water varied inversely with size. The data are discussed in relation to the distinction between smolting and non-smolting salmonid species.

INTRODUCTION

THE ANADROMOUS SALMONIDAE appear to fall into two broad categories with respect to age-based variation in ability to survive transfer from fresh water into sea water. The first group of species, represented by *Oncorhynchus kisutch*, *Salmo salar*, *S. trutta* and *S. gairdneri*, include fish unable to resist sea water as underyearlings, but able to adapt to this environment at later stages (Huntsman and Hoar, 1939; Black, 1951; Parry, 1958). By contrast the second group, which includes *O. keta*, *O. gorbuscha* and possibly *O. nerka*, displays not only the ability to survive direct transfer into sea water in the fry stage (Black, 1951; Houston, 1959a) but also an active preference for this medium when given a choice between fresh and sea water (Houston, 1957; Baggerman, 1960a).

The development of ability to osmoregulate in sea water is correlated, in the first group of species, with the phenomenon of parr–smolt transformation. This process is accompanied by major variations in growth, metabolic activity and patterns of behaviour (Hoar, 1939, 1953, 1958, Baggerman, 1960b). Of particular interest from the viewpoint of sustained survival in sea water is the development at this time of the so-called “chloride secretory cells”; units believed to be the site of extrarenal electrolyte excretion in animals adapted to sea water (Hoar, 1951; Nishida, 1953; Parry, 1958). These observations together with data indicating marked decreases in plasma and tissue electrolyte levels of fish held in fresh water (Fontaine, 1951; Houston, 1959b, 1960) suggests that the animals at this stage undergo premigratory adaptation to the osmoregulatory requirements of marine life.

There is little evidence to suggest a comparable series of changes in the second group of species. Investigations by Black (1951) on the adaptation of

¹Received for publication September 3, 1959; as revised, January 4, 1961.

²Contribution from the Department of Zoology and the Institute of Fisheries of the University of British Columbia, with financial assistance from the National Research Council.

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chum salmon fry to sea water, by Hoar (1958) and Houston (1957) on the behaviour of chum, pink and sockeye fry, and by Skud (1955) on the length-weight relationship of juvenile pink salmon do not indicate premigratory changes equivalent to those seen in the smolting salmonids. The species of this second category are thought by Hoar (1958) to represent an evolutionary trend toward the abbreviation of the freshwater phase of life, and a loss of parr-smolt transformation.

While major variations in the sea water tolerance of parr and smolt stages of smolting species are well established, little attention has been directed toward possible variations in adaptive ability during the relatively short interval during which the outward characteristics of the smolt stage develop. The present study constitutes a preliminary investigation of this point in a typical smolting species, the steelhead trout (*Salmo gairdneri*). Estimates of adaptive ability have been based upon the time required for animals believed to represent the smolt and post-smolt stages to reduce the increases in plasma and tissue chloride levels which result from transfer into sea water. Because few small trout were available, no attempt has been made to assess the osmoregulatory capacities of the parr and silvery-parr stages. For purposes of comparison a similar investigation has been made of size-related variations in the ability of a typical non-smolting species, the chum salmon (*Oncorhynchus keta*), to adapt to sea water.

MATERIALS AND METHODS

STOCKS. Steelhead trout used in this investigation were obtained from the Smith's Falls (Cultus Lake) Hatchery of the British Columbia Game Commission. Chum salmon stocks were obtained through the courtesy of Dr Ferris Neave of the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C. Both species were maintained at the University in running, dechlorinated water and were fed a commercial dry diet (Clark's Fish Food) supplemented with cod liver oil and yeast. Growth was good, and following the "delayed mortality" commonly encountered after transportation few deaths occurred in either group during the experimental period (May, June, July, 1957). Water temperature varied from 10 to 16°C over the period of maintenance and the fish were held under normal spring and summer conditions of light in the laboratory.

ACCLIMATION TO SEA WATER. Groups of 10 to 20 fish were acclimated to sea water in approximately 50-litre wooden boxes floated in constant temperature units and held at $10.0 \pm 0.2^\circ\text{C}$. The fish were transferred in water from hatchery troughs to acclimation tanks and a period of 35 to 40 hours allowed for recovery from any shock of handling. The fresh water was then drained off to a depth of 8 cm and replaced with sea water from an overhead reservoir. Reservoir concentrations were adjusted so that a salinity of 22 to 24 parts per thousand was achieved in the acclimation tanks. Precaution was taken not to disturb the animals during transfer into the tanks, and during replacement of fresh water

with sea water, in order to avoid the initiation of "laboratory diuresis" and other conditions of electrolyte imbalance resulting from handling procedures (Meyer, 1948; Forster and Berglund, 1956).

SAMPLING. Steelhead trout were anesthetized prior to sampling in aqueous tricaine methanesulphonate (MS-222). Individual fish were loosely mounted ventral side uppermost upon a frame and blood samples drawn from the exposed bulbus arteriosus into heparinized and dried syringes. Muscle samples were excised from the dorsal fin area of the epaxial muscle band, rapidly dissected free of obvious fat, skin, cartilage and bone, and refrigerated until required in air-tight moist chambers.

Since chum salmon were too small to allow separate sampling of plasma and tissue, whole body chloride determinations were carried out. Fry were killed by a sharp blow on the head, rinsed twice in distilled water, lightly blotted with paper towelling and stored in the same manner as muscle samples.

ANALYTICAL PROCEDURES. Plasma chloride was estimated by the method of Schales and Schales (1941), and tissue chloride by the modified "open Carius" procedure proposed by Manery (1955). Details of these procedures have been described in an earlier publication (Houston, 1959b).

TREATMENT OF DATA. Changes in chloride concentration during adaptation to sea water have been related to the following variables: steelhead trout—weight, fork length, coefficient of condition; chum salmon—weight, fork length. Regression equations describing variations in plasma and tissue levels of chloride with each factor were calculated for fish adapted to fresh water, and for each acclimation period in sea water. Ability to regulate in sea water has been related to morphological characters believed to describe the smolt and post-smolt phases of development. Original determinations are tabulated in Houston (MS, 1958).

RESULTS

STEELHEAD TROUT

Assessment of steelhead trout as smolt or post-smolt has been based principally upon variations in length-weight relationship and changes in plasma chloride concentrations with weight. Figure 1 indicates a gradual decrease in the slope of the length-weight relationship with the most abrupt variation occurring between 35 and 45 g, and 16.5 to 17.5 cm. Within this range of lengths and weights, coefficients of condition varied from 0.55 to 0.75. In fish larger than 45 g the condition factor increased steadily with weight to a maximum of about 1.10 in fish heavier than 200 g. Too few data were available to allow precise estimates to be made of the range of condition factors in fish smaller than 30 g, but most values were greater than 0.7, suggesting that a decrease in condition accompanied parr-smolt transformation (followed by an increase when this was completed, at least under artificial conditions). In general the variations noted resembled those observed by Hoar (1939) for the weight, length and

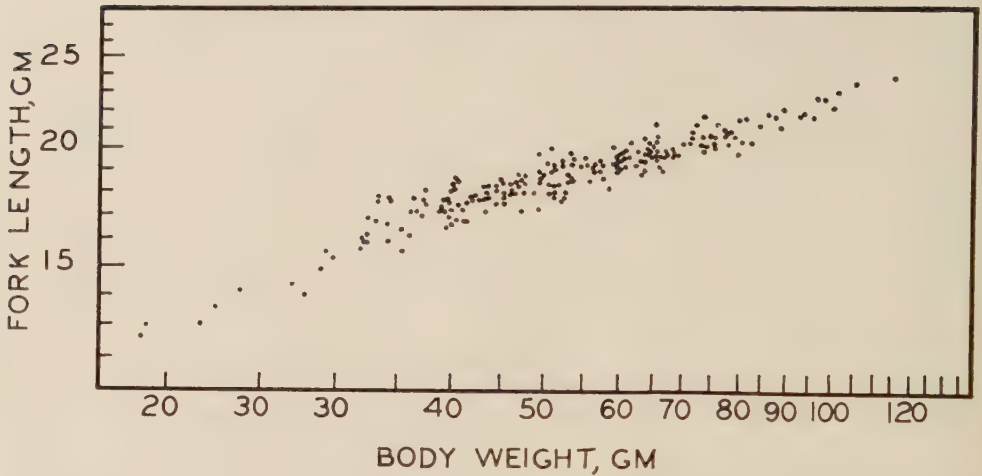


FIG. 1. Length-weight relationship of steelhead trout used in the experiments.

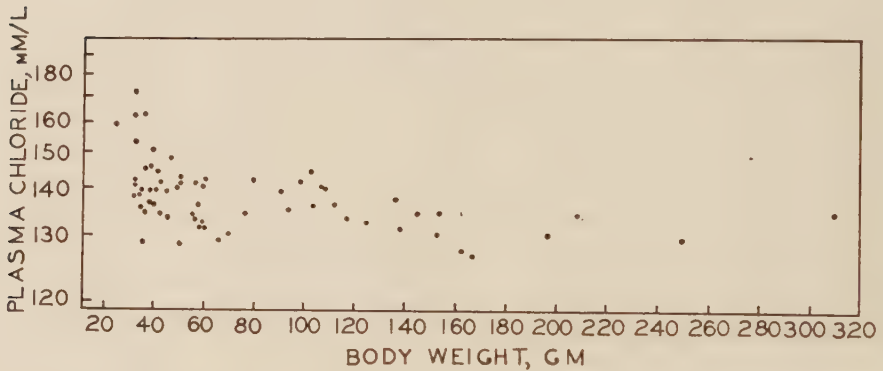


FIG. 2. Variation in plasma chloride concentration with weight in steelhead trout held in fresh water.

condition of Atlantic salmon, and by Kobayashi and Mogami (1958) for condition factor of rainbow trout (*S. irideus*).

In addition to the occurrence of a variation in the growth pattern, other data support the assumption that steelhead with the length, weight and condition-factor values characteristic of the inflection range were in the smolt phase of development. Figure 2 relates variations in plasma concentrations of chloride to weight in animals maintained in fresh water. Chloride levels decreased with increase in weight, with the most pronounced variations taking place between 40 and 55 g, or at about the same weight range within which the length-weight range changed most abruptly. Premigratory decreases in plasma and tissue electrolyte concentrations have been observed in several anadromous species (Fontaine, 1951; Kubo, 1955; Houston, 1960) and may be correlated with variations in blood levels of endocrine products related to electrolyte metabolism

(Fontaine and Hatey, 1954). It would appear reasonable to attribute these observations to the development and activity of "chloride-secretory cells", which is marked at about this stage of development in several migratory salmonids (Hoar, 1951; Nishida, 1953; Parry, 1958).

The studies of Maher and Larkin (1954) on the steelhead trout population of the Chilliwack River, British Columbia, also provide some support for the assumption. These authors found that downstream migrants of the same age-group (2 years) as those used in the present study had a mean fork length of 16.49 cm. It may be assumed that these animals were in the smolt stage of development. Reference to Fig. 1 indicates that this value is very close to the inflection point of the weight-length curve of the present steelhead population, and well within the range believed to be characteristic of the smolt phase of this group of trout.

On the basis of the foregoing data the following parameters have been taken as describing the smolt and post-smolt stages:

Smolt: fork length, 17 cm; weight, 40 gm; condition factor, 0.7.

Post-smolt: fork length, 20 cm; weight, 70 gm; condition factor, 0.9.

Tables I and II and Figs. 3 and 4 summarize changes in plasma and tissue levels of chloride computed for each of the above fish sizes, following transfer of the trout from fresh water into sea water. In each instance increases in chloride level accompanied transfer into sea water. Since fewer than 5% of the fish died during acclimation it may be assumed that the changes in internal electrolyte concentrations were within the tolerance limits of the species and constituted the adjustive phase of adaptation to sea water.

Increases in plasma chloride were consistently greater in fish believed to represent the post-smolt stage than in those assumed to be smolts. This was most apparent with respect to condition. Trout characterized by a coefficient of condition of 0.7 exhibited a maximum increase of 14.8%, while that in fish of condition factor 0.9 was 26.3%. The maximum weight-related increase in plasma concentration in post-smolts was 29.4%, while that for length was 29.1%. Comparable values for smolts were 23.3 and 17.1% respectively.

The duration of increased plasma and tissue electrolyte levels and presumably of the adjustive phase of adaptation, was in each instance longer in post-smolts than in the smolts. At the final period of observation (168 hours), or before that time, the latter group displayed plasma concentrations lower than those observed in fresh water. At the same time post-smolt chloride levels were generally above the levels recorded in fish of similar size in fresh water. Extrapolation of the downward arms of the chloride-time curves suggested that these animals would require from 200 to 240 hours to achieve freshwater levels.

The degree and duration of deviations in plasma levels of chloride suggests, then, that steelhead in the post-smolt stage were less efficient in their adaptation to sea water than were those in the smolt stage.

TABLE I. Plasma chloride (pCl) changes in steelhead trout in sea water as related to weight, fork length, and coefficient of condition. In the regression equations, Y-values represent plasma chloride in millimoles per litre (mM/l); X-values represent respectively weight in grams (W), fork length in centimetres (FL), and coefficient of condition ($C = 100$ times weight in grams divided by the cube of fork length in centimetres).

A: Plasma Chloride versus Weight					
Hours in sea water	Regression equation	W = 40 g (smolts)		W = 70 g (post-smolts)	
		pCl	% change	pCl	% change
0	$Y = 152.8 - 0.3X$	140.8		131.8	
4	$Y = 159.8 - 0.2X$	151.8	+ 7.8	145.8	+ 10.6
10	$Y = 172.0 - 0.3X$	160.0	+ 13.6	151.0	+ 14.6
15	$Y = 172.7 - 0.2X$	164.7	+ 17.0	158.7	+ 20.4
22	$Y = 163.0 - 0.1X$	159.0	+ 12.9	156.0	+ 18.4
36	$Y = 177.6 - 0.1X$	173.6	+ 23.3	170.6	+ 29.4
86	$Y = 170.6 - 0.1X$	166.6	+ 18.3	163.6	+ 24.1
126	$Y = 147.9 + 0.03X$	146.7	+ 4.2	145.8	+ 10.6
168	$Y = 136.9 + 0.08X$	133.7	- 5.0	131.3	- 0.4

B: Plasma Chloride versus Fork Length					
Hours in sea water	Regression equation	FL = 17 cm (smolts)		FL = 20 cm (post-smolts)	
		pCl	% change	pCl	% change
0	$Y = 187.1 - 2.6X$	142.9		135.1	
4	$Y = 155.9 - 0.5X$	147.4	+ 3.2	145.9	+ 8.0
10	$Y = 209.9 - 2.7X$	164.0	+ 14.8	155.9	+ 15.4
15	$Y = 238.0 - 4.3X$	164.9	+ 15.4	152.0	+ 12.5
22	$Y = 186.1 - 1.4X$	162.3	+ 13.6	158.1	+ 17.0
36	$Y = 108.4 + 3.3X$	164.5	+ 15.1	174.4	+ 29.1
86	$Y = 204.8 - 2.2X$	167.4	+ 17.1	160.8	+ 19.0
126	$Y = 157.7 - 0.3X$	152.6	+ 6.9	151.7	+ 12.3
168	$Y = 126.6 + 0.8X$	140.2	- 1.8	142.6	+ 5.6

C: Plasma Chloride versus Coefficient of Condition					
Hours in sea water	Regression equation	C = 0.7 (smolts)		C = 0.9 (post-smolts)	
		pCl	% change	pCl	% change
0	$Y = 226.7 - 105.8X$	152.6		131.5	
4	$Y = 176.1 - 37.5X$	149.8	- 1.8	142.3	+ 8.2
10	$Y = 108.6 + 63.7X$	153.2	+ 0.4	165.9	+ 26.2
15	$Y = 78.1 + 97.8X$	147.6	- 3.3	166.1	+ 26.3
22	$Y = 157.5 + 2.3X$	159.1	+ 4.3	159.6	+ 21.2
36	$Y = 213.6 - 54.8X$	175.2	+ 14.8	164.3	+ 24.9
86	$Y = 159.7 + 4.6X$	162.9	+ 6.7	163.8	+ 24.6
126	$Y = 136.2 + 21.2X$	151.0	- 1.0	155.3	+ 18.1
168	$Y = 138.5 + 4.7X$	141.8	- 7.1	142.7	+ 8.5

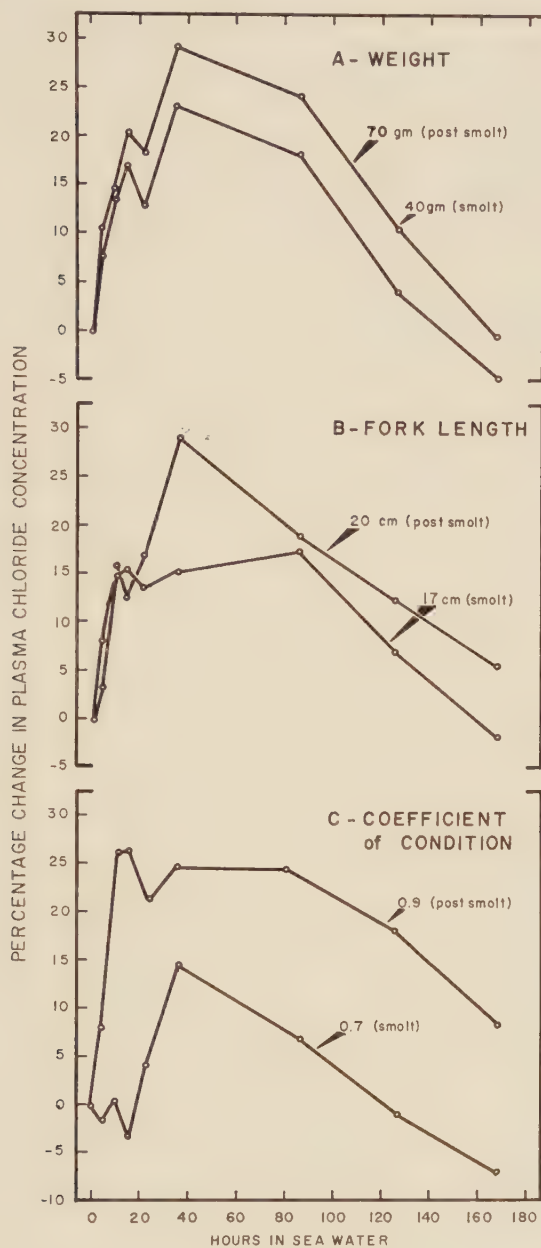


FIG. 3. Relation of percentage increase in plasma chloride (above the freshwater level) to length of exposure to sea water, for steelhead smolts and post-smolts as defined by three indices (weight, length and coefficient of condition).

Differences in tissue chloride levels between the two groups were equally conspicuous. While the duration of the period of raised chloride concentrations was about the same in smolts and post-smolts, the latter took up relatively more chloride than did the former. Since chloride ion is largely confined to the extra-cellular compartment and does not readily undergo osmotic inactivation by complex formation (Manery, 1954) it would appear likely that variations in tissue fluid distribution are relatively more marked in post-smolts, and that these fish underwent a greater degree of stress during adaptation than did smolts.

TABLE II. Tissue chloride (tCl) changes in steelhead trout in sea water as related to weight, fork length, and coefficient of condition. In the regression equations, Y-values represent tissue chloride in millimoles per kilogram of fresh tissue; X-values are as in Table I.

A: Tissue Chloride versus Weight					
Hours in sea water	Regression equation	W = 40 g (smolts)		W = 70 g (post-smolts)	
		tCl	% change	tCl	% change
0	$Y = 31.9 - 0.2X$	23.9		17.9	
4	$Y = 24.6 + 0.2X$	32.6	36.4	38.6	115.6
10	$Y = 44.1 - 0.2X$	36.1	51.1	30.1	68.2
15	$Y = 56.1 - 0.4X$	40.1	67.8	28.1	57.0
22	$Y = 37.8 - 0.01X$	37.7	57.7	37.1	107.3
36	$Y = 53.5 - 0.3X$	41.5	73.6	32.5	81.6
86	$Y = 30.3 - 0.1X$	26.3	10.0	23.3	30.2
126	$Y = 34.5 - 0.1X$	30.5	27.6	27.5	53.6

B: Tissue Chloride versus Fork Length					
Hours in sea water	Regression equation	FL = 17 cm (smolts)		FL = 20 cm (post-smolts)	
		tCl	% change	tCl	% change
0	$Y = 48.7 - 1.4X$	24.9		20.7	
4	$Y = -21.2 + 2.9X$	28.1	12.9	36.8	77.8
10	$Y = 69.8 - 1.8X$	39.2	57.4	33.8	63.3
15	$Y = 64.1 - 1.5X$	38.6	55.0	34.1	64.7
22	$Y = 46.3 - 0.5X$	37.8	51.8	36.3	75.4
36	$Y = 96.5 - 3.0X$	45.5	82.7	36.5	76.3
86	$Y = 34.5 - 0.5X$	26.0	4.4	24.5	18.4
126	$Y = 15.0 + 0.7X$	26.9	8.0	29.0	40.1

C: Tissue Chloride versus Coefficient of Condition					
Hours in sea water	Regression equation	C = 0.7 (smolts)		C = 0.9 (post-smolts)	
		tCl	% change	tCl	% change
0	$Y = 40.3 - 20.9X$	25.7		21.5	
4	$Y = 56.7 - 20.5X$	42.3	64.6	38.2	77.8
10	$Y = 49.7 - 19.6X$	36.0	40.1	32.1	49.3
15	$Y = 40.6 - 5.9X$	36.5	42.0	35.3	64.2
22	$Y = 24.7 + 15.9X$	35.8	39.3	39.0	81.4
36	$Y = 61.5 - 28.2X$	41.8	62.7	36.1	67.9
86	$Y = 28.5 - 4.4X$	25.4	-1.2	24.5	14.0
126	$Y = 62.8 - 46.2X$			21.2	-1.4

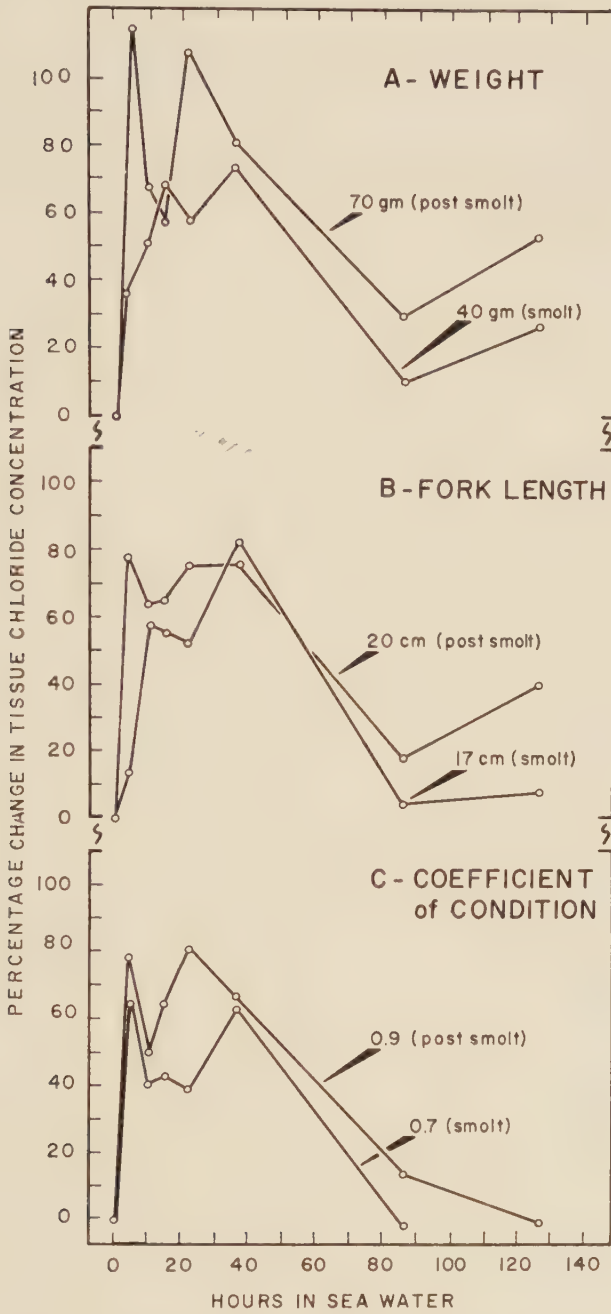


FIG. 4. Relation of percentage increase in tissue chloride (above the freshwater level) to length of exposure to sea water, for steelhead smolts and post-smolts as defined by three indices (weight, length and coefficient of condition).

CHUM SALMON

Figure 5 indicates the variation of length with weight in chum salmon fry maintained in fresh water. Over the weight range of the population there was no indication of inflection, and no morphological basis for suggesting the occurrence of a transformation comparable to that seen in steelhead trout and the other

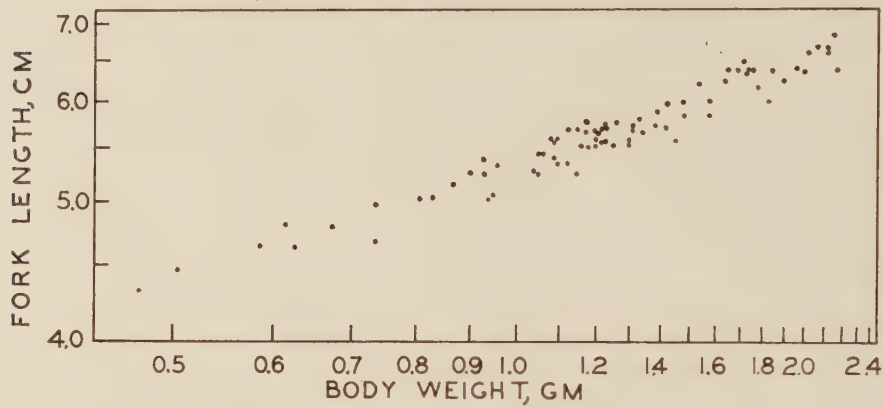


FIG. 5. Length-weight relationship of chum salmon fry used in the experiments.

TABLE III. Total body chloride (tot. Cl) changes in chum salmon fry in sea water as related to fork length and weight. In the regression equations, Y-values represent total body chloride in millimoles per kilogram of fresh tissue; X-values represent respectively fork length in millimetres (FL) and weight in grams (W).

A: Total Body Chloride versus Fork Length					
Hours in sea water	Regression equation	FL = 50 mm		FL = 60 mm	
		tot. Cl	% change	tot. Cl	% change
0	$Y = 110.3 - 0.6X$	80.3		74.3	
3.5-4.5	$Y = 262.6 - 2.9X$	117.6	46.5	88.6	19.2
10-10.5	$Y = 240.9 - 2.4X$	120.9	50.6	96.9	30.4
14.5	$Y = 278.5 - 2.8X$	138.5	72.5	110.5	48.7
24	$Y = 220.4 - 2.2X$	110.4	37.5	88.4	19.0
37	$Y = 229.3 - 2.3X$	114.3	42.3	91.3	22.9

B: Total Body Chloride versus Weight					
Hours in sea water	Regression equation	W = 0.9 g		W = 1.6 g	
		tot. Cl	% change	tot. Cl	% change
0	$Y = 84.5 - 6.9X$	78.3		73.5	
3.5-4.5	$Y = 128.5 - 23.9X$	107.0	36.7	90.3	22.9
10-10.5	$Y = 149.1 - 33.0X$	119.4	52.5	96.3	31.0
14.5	$Y = 188.4 - 50.3X$	143.1	82.8	107.9	46.8
24	$Y = 138.1 - 37.4X$	104.4	33.3	78.3	6.5
28	$Y = 138.2 - 35.5X$	106.2	35.6	81.4	10.8
37	$Y = 140.8 - 34.5X$	109.7	40.1	85.6	16.5

smolting species. A similar conclusion may be drawn from data provided by Skud (1955) on the pink salmon which also migrates within a few months after hatching. Other physiological, morphological and ethological data assembled by Hoar (1958) also lead to the conclusion that smolt transformation does not occur in chum and pink salmon.

Transfer from fresh water into sea water resulted in sharp changes in whole body levels of chloride (Table III, Fig. 6). As with steelhead, mortality was

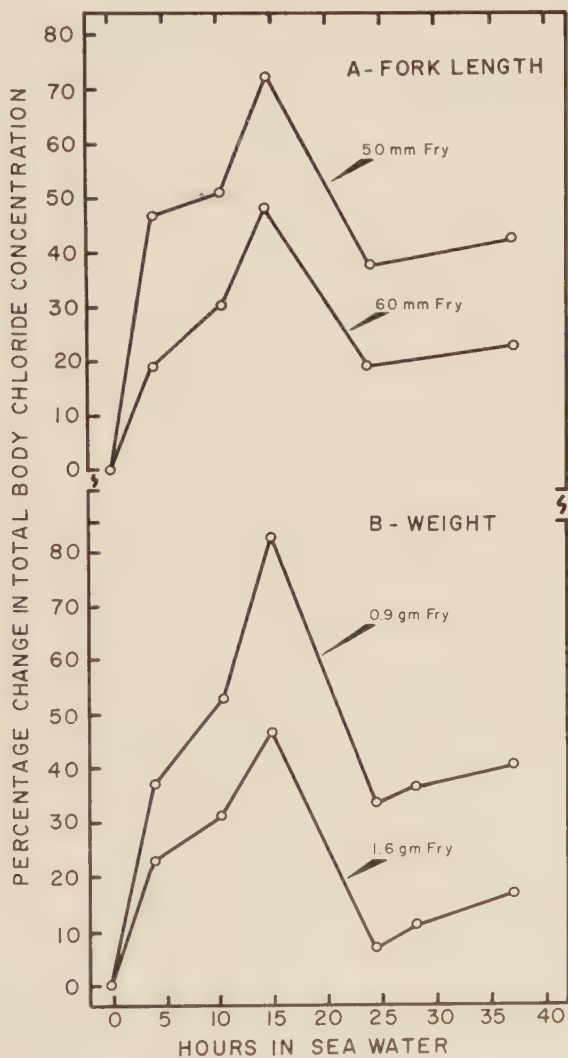


FIG. 6. Relation of percentage increase in total body chloride (above the freshwater level) to length of exposure to sea water, for chum salmon fry of two lengths.

slight during acclimation and changes in concentration are believed to reflect adjustive responses. The adjustive phase of adaptation lasted for 24 to 28 hours in these fish. A similar pattern of adaptation has been observed by Black (1951) for the same species.

In contrast to the situation observed in steelhead, increase in both fork length and weight was accompanied by a *decrease* in maximum uptake. Growth increases adaptive efficiency, indicating that some morphological relationship (e.g., exposed permeable surface area to body mass ratio) may play a greater role than a particular physiological condition, in the rapidity with which this species adapts to sea water.

DISCUSSION

While the general pattern of adaptation to sea water is comparable in both the steelhead trout and chum salmon, a major difference is seen in the influence of size. In the non-smolting species growth enhances osmoregulatory adaptability. This observation, together with data on changes in body chloride levels of freshwater forms, suggests that the juveniles while still in fresh water become increasingly preadapted to the osmoregulatory necessities of marine life. Presumably such preadaptation would include the development and activation of some extrarenal electrolyte excretory mechanism such as that postulated to exist in the gills.

The shift in osmotic adaptability appears to be unidirectional in both chum and pink salmon. In this laboratory chum salmon, and more noticeably pink salmon, have died if held in fresh water for longer than 7 or 8 months after hatching. Similarly Black (1951) observed that chum salmon maintained in freshwater underwent heavy mortality beginning in mid-August, accompanied by increases in water content and decreases in density. These observations and those of Ford (1958) on the numbers of glomeruli in the kidneys of freshwater-maintained pink salmon fry as compared to those of animals held in sea water suggest that death was due, at least in part, to loss of ability to regulate water and electrolyte levels. Although some workers have been able to hold pink salmon fry in fresh water for considerable periods of time (personal communication from W. E. Ricker), nevertheless there is some basis for assuming that movement into sea water is obligative for the non-smolting juvenile salmon.

In contrast to this situation in the non-smolting forms, many of the smolting species appear to be more facultative in their habitat requirements. In steelhead trout and in other species of this group seaward migration may occur after 2, 3, or even 4 years of freshwater life, and several of these species are represented by wholly freshwater varieties (e.g.: *O. nerka*, *S. salar*, *S. gairdneri*). While parr-smolt transformation results in the development of the regulatory systems required for marine osmoregulation, it does not necessarily result in the complete

loss of ability to survive in fresh water. The decreased adaptive efficiency of the post-smolts, however, suggests that adaptability to sea water varies on a seasonal basis. Corroborative evidence for this contention is available in studies indicating seasonal variations in the responses of sockeye and coho salmon fry and smolts to sea water (Houston, 1957; Hoar, 1958; Baggerman, 1960a), and in thyroid activity (Baggerman, 1960b). If this is the case, one might expect the occurrence of somewhat more complicated patterns of endocrinological function in the smolting forms. The resulting lability of the smolting species in regard to their osmotic habitat requirements may be a factor of definite survival value in the face of local conditions blocking downstream migration.

From the evolutionary point of view the observed variations in osmoregulatory ability with size, and inferences of obligative and facultative habitat requirements in the smolting and non-smolting species support the contention of Hoar (1958) that chum and pink salmon represent a branch of salmonid development which has diverged farther from the ancestral stock than has that represented by the present day smolting group of species.

From the more immediate viewpoint of the hatchery production of commercially desirable species such as the steelhead trout and Atlantic salmon, the data suggest that further investigation of the influence of size on adaptability to sea water would be desirable. Earlier investigations (Houston, 1959a) have shown that during adaptation to sea water the locomotor performance of salmonids is depressed. This effect is significantly correlated with the initial adjustive responses of the animals to sea water; increased plasma electrolyte concentrations, uptake and loss of cellular cations, and redistribution of tissue fluids. During this phase of locomotor depression the migrants may be more vulnerable to the action of predators. Thus release of hatchery fish at the weight and length producing most efficient adaptation to sea water should reduce both the extent and duration of adjustive changes and hence susceptibility to predation. Similarly, delays in downstream movement of either hatchery-reared or wild populations of salmonids by natural or artificial obstacles (e.g. power or other dams) are to be avoided wherever possible. Prolonged lack of feeding prior to entry into the sea, together with development of post-smolt changes in osmoregulatory mechanisms, may be expected to result in lack of efficiency in sea water, or the loss of ability to adapt successfully to the marine environment.

ACKNOWLEDGMENTS

The author is indebted to Professor William S. Hoar who supervised the investigation and read the manuscript. Dr P. A. Larkin and Dr C. C. Lindsey were most generous in their advice and assistance during the study.

Financial support from the National Research Council in the form of studentships made the investigation possible.

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Comparison of Largest Great Slave Lake Fish With North American Records¹

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ABSTRACT

The largest sizes for 11 of 25 species of Great Slave Lake fish are presented from material collected during studies dating from 1944 and other sources. The North American size records compiled from a literature search also are given. Only two of the Great Slave Lake records exceed the existing North American ones. It is suggested that the maximum size of fish is not attained among unexploited populations in oligotrophic lakes.

INTRODUCTION

INTEREST IN THE maximum size of fish is not restricted to anglers, because this information is contained in nearly all regional and general books on fish. The Great Slave Lake records for 11 of the 25 species in the Lake are presented and compared with the published North American records.

GREAT SLAVE LAKE RECORDS

A program has been carried out annually at Great Slave Lake by the Fisheries Research Board of Canada since 1944—see Keleher (1959) for a brief review and bibliography—and it is from these data that a compilation has been made. No systematic effort has been made previously to acquire such information, so it is possible that some fish taken by the commercial fishermen and others would have exceeded the present listings. The maximum size and other particulars are presented in Table I. Weight is the size criterion since most of the data are in this form. Records from other sources which exceed our own have been included, but we have in every instance listed the largest fish weighed by a Board employee.

The record for inconnu, *Stenodus leucichthys* (Güldenstädt), has been published (Rawson, 1947) and that for the longnose sucker, *Catostomus catostomus* (Forster), was provided by Dr R. H. D. Harris from his unpublished thesis.

¹Received for publication November 7, 1960.

TABLE 1. Records of the largest fish caught from Great Slave Lake. The footnotes indicate information not obtained by the Fisheries Research Board of Canada. See Kennedy, 1956, figure 6, for the lake divisions listed in the "Area" column.

Species	Weight	Fork length	Date	Area	Location	Caught by	Data from
	<i>lb</i>	<i>in</i>					
Lake whitefish	22.0	10.0	...	1958	H Gros Cap	J. Kashak	Adolph Maerz ^a
"	16.0	7.0	...	1950	M Blanchet Is.	A. Koziel	J. A. Dick (FRB)
Round whitefish	4.5	2.0	Aug. 1, 1956	N	S. of Pearson Pt.	G. Whiteley	H. Hamp (FRB)
Luciomet	55.0	25.0	...	1943?	A Big Buffalo R.	Wm. Greer	Wm. Greer ^b
"	54.7	24.8	Jan. 4, 1960	K	61° 41' N, 112° 52' W.	Wm. Janus	K. G. Roberts, C. G. Haight (FRB)
Lake trout	66.5	30.2	...	...	...	J. McCordic	G. Carter ^c
"	66.0	29.9	...	...	SE of Long Is.	R. Helmer	R. M. Hanson (FRB)
Arctic Grayling	5.0	2.3	...	...	O McKinley R. mouth	W. G. Clark	M. Ball ^d
"	4.1	1.9	...	...	H Campbell Bay	D. Kirkness	H. Hamp (FRB)
Goldeye	2.6	1.2	...	...	A Sulphur Pt.	...	F. Bastian (FRB)
Northern pike	30.0	13.6	...	...	F West Mirage Is.	C. Courtoreille	J. Dowling (FRB)
Longnose sucker	7.3	3.3	...	...	D Slave Pt.	Wm. Weselowski	R. H. D. Harris (FRB)
White sucker	6.7	3.0	...	...	F 10 miles NW Ptarmigan Pt.	D. C. Scott	D. C. Scott (FRB)
Burbot	18.5	8.4	...	...	E Redrock Pt.	M. Fedorus	J. Sunley (FRB)
Walleye	11.0	5.0	...	...	B 20 miles SE Outpost Is.	Moneias Bros.	G. Anderson (FRB)

^aForeman, McInnes Products Corporation.

^bResident, Big Buffalo River; personal communication to Dr D. S. Rawson.

^cCarter Fisheries Ltd.; specimen in possession of R. W. Park, Park-Hannesson Ltd., Winnipeg.

^dFishing contest editor, *Field and Stream*.

NORTH AMERICAN RECORDS

With the exception of the angling contest records started in 1911 by *Field and Stream* (Anon., 1960), maximum sizes of North American freshwater fish only can be found by a search of the literature. Our search probably has not been complete, but presentation of the results may encourage other contributions to this subject.

The maximum size reported for a lake whitefish, *Coregonus clupeaformis* (Mitchill), is 42 lb. According to Louis P. Hogstad of Duluth, Minnesota, it was caught about 1918 at Isle Royale in Lake Superior (Van Oosten, 1946). No other records exceeding 26 lb have been located. Koelz (1929) and Van Oosten (1946) mentioned reports of lake whitefish attaining this size in the Great Lakes. The report (Anon., 1946; Derback, 1947) of a 26 lb lake whitefish being taken in Manitoba during the 1923–24 fishing season should no longer be accepted. This fish, captured in Sturgeon Bay, Lake Winnipeg, actually weighed 24 lb (G. E. Butler, personal communication, 1960).

The round whitefish, *Prosopium cylindraceum* (Pallas), is considerably smaller than the lake whitefish. The maximum reported has been about 5 lb for a Lake Superior fish (Koelz, 1929).

Wynne-Edwards (1952) pointed out that inconnu attain a larger size in the USSR, where a weight of 88 lb (40 kg) has been recorded, than they do in North America. Here the two heaviest fish have been "just over 63" lb and 56.5 lb (Dymond, 1943).

With respect to the size of lake trout, *Cristivomer namaycush* (Walbaum), Dr S. Mitchill stated at Michilimackinac in Lake Huron one was known to attain 120 lb (Richardson, 1836). Other credible records are much less. An 88 lb lake trout was caught at Grand Haven, Michigan, in 1864 (Goode, 1884). In 1906 an 87 lb lake trout was taken on rod and reel from Lake Bennett, Yukon Territory (Anon., 1953). Mr T. Goodman of Fairford, Manitoba, netted an 80.5 lb fish in Lake Athabasca on September 11, 1955. It was photographed (Symington, 1958) and is now on display at the Saskatchewan Museum of Natural History, Regina. The angling record is a Lake Superior fish of 63.1 lb, caught in 1952.

Prior to 1959 about 4 lb appeared to be the North American limit for Arctic grayling, *Thymallus arcticus* (Pallas). The fishing contest editor for *Field and Stream* informs me (M. Ball, personal communication, 1960) that a new angling record of 5.0 lb has been accepted from Great Slave Lake (Table I). The previous angling record, dating from 1955, was 4 lb from the Clearwater River, Saskatchewan. Manchester (1954) stated that the largest grayling on record, weighing "over four pounds", came from Wrigley Harbour, Great Slave Lake. However, he has advised me (personal communication, 1959) that this statement cannot now be substantiated.

The upper size limit of the goldeye, *Amphiodon alosoides* Rafinesque, is about 3 lb. The largest specimen cited by Trautman (1957) was a 3.1 lb female. One caught in the North Platte River, Wyoming, weighed 2.7 lb (Simon, 1946).

Northern pike, *Esox lucius* Linnaeus, from North America appear not to exceed 50 lb. Chambers (1896) saw a 49 lb pike from Lac Tschotagama, Quebec, in 1890. The *Field and Stream* angling record is 46.1 lb for one taken from a New York reservoir in 1940.

Neither the longnose sucker nor the white sucker, *Catostomus commersoni* (Lacépède), attain a large size. Longnose suckers weighing 5 lb were "not uncommon" in Lake Abitibi in 1925 (Dymond and Hart, 1927), but the 7.3 lb specimen from Great Slave Lake is apparently the record. White suckers previously had seemed the larger species: Webster (1942) reported a 6.9 lb white sucker from East Twin Lake, Connecticut, in 1939. A 6.5 lb white sucker was caught in Maine in 1957 (Everhart, 1958).

The burbot, *Lota lota* (Linnaeus), can attain a weight of 75 lb according to Wynne-Edwards (1952). The record for North America presumably is Dall's (1870) listing of 60 lb for Alaska.

Most authors report 25 lb as the maximum for the walleye, *Stizostedion vitreum* (Mitchill), probably on the basis of Goode's (1884) statement. An Associated Press news release stated that a 25 lb walleye was caught on August 2, 1960, at Old Hickory Lake, Tennessee, by a Nashville angler, Marby Harper. If substantiated, this would be the new angling record.² The existing one is for a 22.2 lb fish caught at Fort Erie, Ontario, in 1943. In 1950 a 23.6 lb walleye was caught in the Moon River, Ontario (Scott, 1954).

DISCUSSION

With the exception of the Arctic grayling and longnose sucker, none of the records for Great Slave Lake fish exceed in weight those caught elsewhere. The round whitefish and white sucker records are near the maximum reported but the remainder are much less. Of the present Lake records, none were fish taken during the Board's general survey from 1944 to 1947, when about 12,000 fish were examined (Rawson, 1951). This suggests that fish do not attain their maximum size under these conditions—that is, among relatively unexploited fish populations in an oligotrophic lake. The *Field and Stream* article (Anon., 1960) substantiates this conclusion.

Two of the North American records cited seem doubtful. These are 42 lb for lake whitefish and 120 lb for lake trout. The disparity between the former and the other known records of 26 lb is too great to be accepted on the evidence presented. Likewise, the 120 lb lake trout far exceeds any other known. While some authors may accept 120 lb lake trout, it is felt this century-old record should be challenged.

ACKNOWLEDGMENTS

While assistance has been received from many individuals, particular acknowledgment should be made to my associate, Mr N. H. F. Watson and to Dr J. Van Oosten.

²This record is now accepted by *Field and Stream*; see the issue of March, 1961, vol. 55, No. 11, p. 71.

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The Lake Trout of Lac la Ronge, Saskatchewan¹

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ABSTRACT

The lake trout, *Salvelinus namaycush*, of Lac la Ronge was studied in the years 1948 to 1959 using gill netting, tagging, creel census and sampling of the spawning run. The trout spawned on shallow rocky reefs in the first week of October, when water temperatures were about 10°C (50°F). Of the spawning run, 82% were from 7 to 12 years old. Possibly 10% of the mature trout failed to spawn in any single year.

Growth rate varied widely in individuals and the average rate produced, at 10 years, a trout of 26 inches (66 cm) fork length and weighing 8 lb (3.6 kg). No difference was found between growth rates of males and females and there was no change in average growth rate during the 10-year study. However, trout in the main lake grew considerably faster during their first 5 years than those in the deeper, colder Hunter Bay. Thirty-three trout weighing from 30 to 43 lb were examined.

Ciscoes, whitefish, ninespine sticklebacks and other fish made up 90% of the food of adult trout. The crustaceans *Mysis* and *Pontoporeia* were eaten in moderate quantities, especially by trout in their third and fourth years. Two cestode parasites were found in the intestine and the larvae of a third in the muscle of trout.

¹Received for publication February 9, 1961.

The trout were widely scattered from break-up of ice in mid-May to late June. As the upper water warmed above 10°C (50°F) they moved down and were concentrated in areas deeper than 20 m (65 ft) during July and August. As the water cooled they again spread into shallow water about mid-September. Of 429 tagged, 60 or 14% were recovered during the first, second and third years after tagging. Recoveries showed extensive movement throughout the lake and a moderate exchange between the main lake and Hunter Bay.

In standard gill-net catches plankton-feeding and bottom-feeding fish outweighed piscivores by 3 to 1 in the main lake and 1.8 to 1 in Hunter Bay. Catch data suggest that the trout population was greater in 1958-59 than in 1948-49. The average size of trout caught and the year-class composition were unchanged after 10 years.

By diverting commercial fishing from trout to whitefish the average commercial catch in the 10-year period has been maintained at 250,000 lb per year, as compared to 316,000 lb in the previous 30 years. The anglers' catch of trout now averages 30,000 lb per year and this could be doubled without exceeding the known capacity of the lake for trout production. The creel census shows no decrease in average size of trout caught, average catch per angler, and number of very large trout taken.

INTRODUCTION

THE LAKE TROUT, *Salvelinus (Cristivomer) namaycush*, is a highly regarded game fish in lakes of northern Saskatchewan. It is also one of the main commercial species, ranking second only to the whitefish in the value of its annual production. It was desirable, therefore, to obtain detailed knowledge of the life history and ecology of this important species in Saskatchewan lakes.

Lac la Ronge was fished commercially and known as a good "trout" lake long before the road made it possible for several thousand anglers to visit it annually. It is probably unique among lakes of this latitude in western Canada in having certain conditions which allow anglers to catch trout readily throughout the summer. The possibility of finding the reasons for this situation added to the scientific interest of the present investigation.

In the 10 years 1948 to 1957, the lake trout were sampled and studied as a part of the program of fisheries research and management on Lac la Ronge. In 1958 and 1959 a more intensive study was carried on, aimed particularly at the seasonal distribution and ecology of the lake trout population. In all years, advantage was taken of the heavy angling for lake trout as revealed by a full-time creel census.

Lac la Ronge, Fig. 1, is a lake of 550 square miles (1425 km²) lying across the southern margin of the Precambrian Shield, and just south of the Churchill River at Latitude 55°. Its general limnology and fisheries were described by Rawson and Atton (1953). By comparison with other large lakes in Saskatchewan Lac la Ronge has been shown to be moderately productive, richer than lakes on the shield but poorer than those on the glacial drift to the south. Lac la Ronge proper can be described as mesotrophic, but Hunter Bay, a 50 square mile part on the east side, is distinctly oligotrophic (Rawson, 1960). Previous studies of the fish of Lac la Ronge include an investigation of the walleye (Rawson, 1957) and the whitefish (Qadri, 1961). The present study continues a plan to investigate each of the major fish species in the lake.

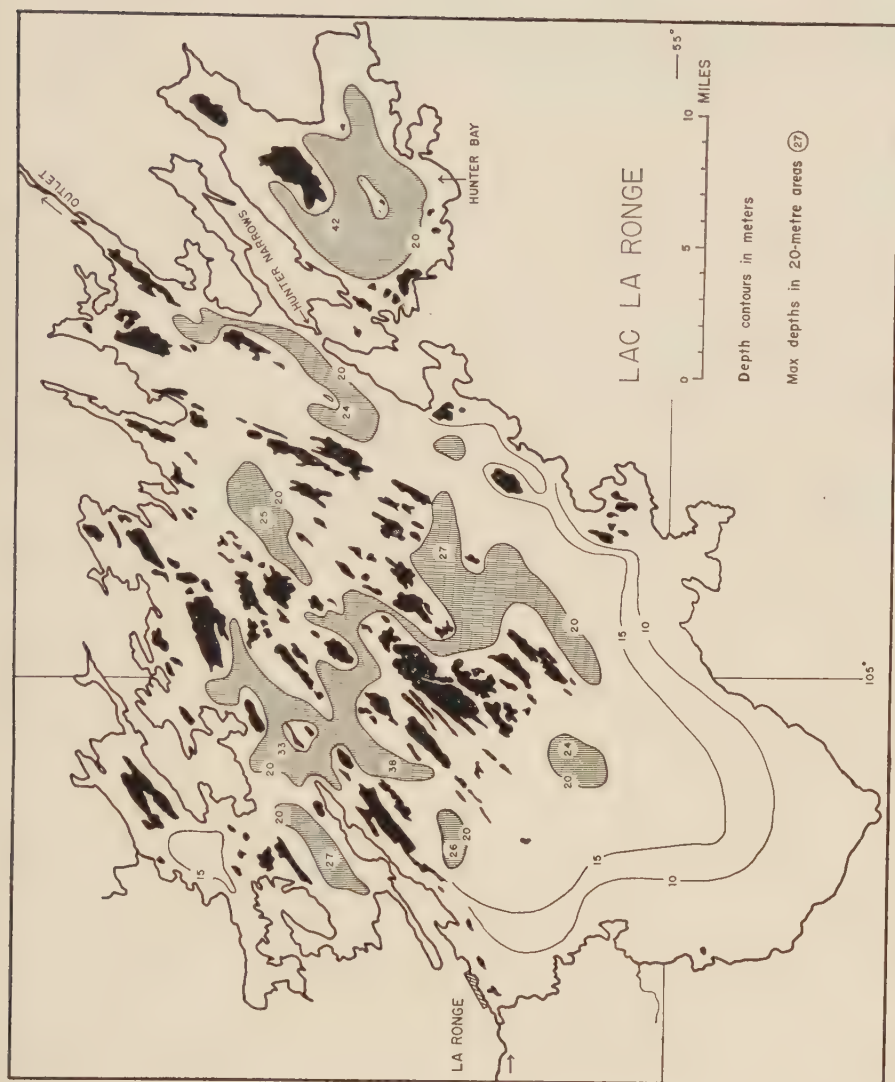


FIG. 1. Map of Lac la Ronge showing the islands, in black, and the areas inside the 20-metre (65 ft) contour, shaded. Lake trout are concentrated in these areas during July and August. For detailed soundings of Lac la Ronge see Chart 6281, Canadian Hydrographic Service, Ottawa.

SPECIFIC IDENTITY AND GEOGRAPHIC DISTRIBUTION

The lake trout is widely distributed across northern North America from Alaska to the Maritime Provinces and from the Great Lakes to some of the Arctic Islands. Unlike many of our northern fish species it has no close relative in Siberia. Walters (1955) and others have suggested that the lake trout entered our northern waters in recent times, coming from a refugium in the Upper Mississippi Valley. Although widespread, the lake trout is not, as stated by Slastenenko (1958), found in "all lakes of sufficient depth to provide cold water in summer".

The occurrence of lake trout in Saskatchewan is restricted to its northern half. It is found in most of the deep lakes on the Precambrian Shield and north of Latitude 55° . It occurs in only a few of the lakes between 54 and 55° . These include Cold Lake on the west boundary, four lakes in the Prince Albert National Park (Rawson, 1936) and East Trout Lake, all of which drain north into the Churchill River. Farther to the east, trout are found in Little Bear, Deschambault, Jan, Hansen and Amisk Lakes, all draining into the Saskatchewan River. Lac la Ronge, lying across the margin of the Precambrian and cut by Latitude 55° , may be regarded as near the southern edge of the typical lake trout area.

In spite of its wide distribution the lake trout appears to be a rather homogeneous species, providing little justification for the recognition of subspecies, with the exception of the siscowet of Lake Superior. The trout of Lac la Ronge are large and well nourished (Fig. 2). Growth studies, reported in a later section, will show that while growth in length of Lac la Ronge trout is much like that of trout in Great Slave Lake, the older fish in Lac la Ronge are considerably heavier than those in Great Slave Lake. It was also found that trout in small lakes near Lac la Ronge often differ considerably in body proportions. The head lengths of adult Lac la Ronge trout average one-fifth of the body (fork) length while trout in MacKay Lake, about 10 miles north of La Ronge, have heads averaging one-quarter of the body length (Fig. 2).

The external colour of Lac la Ronge trout is typically blue-grey to blue-black with occasionally a greenish or brownish cast. The light-coloured spots usually cover an area of 3 to 7 scales. They do not show the light pink or reddish tint often mentioned in descriptions of this species. In some trout, such as the specimen from MacKay Lake shown in Fig. 2, the white spots are large in relation to the dark pigment, thus giving the appearance of a dark reticulum on a light background. The paired and anal fins exhibit varying shades of red and are sometimes quite vivid in colour, contrasting with their white leading edges. The belly is usually silvery or creamy white.

The flesh colour of Lac la Ronge trout ranges from pale creamy white, through light yellow to orange and red. The flesh of immature fish, less than about 17 inches (43 cm) in length, is almost always pale cream or white. Pale shades predominate in adult fish but some individuals exhibit a striking orange or reddish colour. In a preliminary attempt at objective recording of flesh colour, samples of all available flesh colours were collected and frozen. An artist was engaged



FIG. 2. *Above:* Typical lake trout from Lac la Ronge, fork length 27 inches (68.5 cm), weight 9.3 lb (4.2 kg), and age 11 years. *Below:* Large-headed trout from MacKay Lake, fork length 19.3 inches (49 cm), weight 2.9 lb (1.3 kg), and age 8 years. A Lac la Ronge trout of 8 years would be 20% longer and more than double the weight of the MacKay Lake specimen.

to prepare a matching series of colour sheets which were subdivided to provide each worker with a standard set. The five selected standards were described as (1) Creamy white (2) Pale yellow (3) Yellow orange (4) Bright orange. A fifth standard, Orange red, was prepared to match the bright flesh colour of trout from adjacent lakes. However none of the trout examined from Lac la Ronge showed this degree of colour. The approximate rating of our colour standards on the Munsell system of notation was as follows:

1. 3.5 Y 8.6/5.5
2. 9 YR 7.7/6.8
3. 6.5 YR 7.9/9.8
4. 3.5 YR 6.5/11
5. 2.2 YR 6.2/9.2

In the period June 20 to September 15, 1960, flesh colour was recorded for 337 trout taken by anglers on Lac la Ronge. Length, sex and locality was recorded and egg samples were taken from the ovaries of most of the females.

The flesh colours of male and female trout are summarized in Table I. The "pale" coloured fish, numbers 1 and 2, made up 83% of the sample. Males were more numerous among the 17% with "bright" coloured flesh, numbers 3 and 4.

TABLE I. Flesh colour of 337 lake trout 18–31 inches (45.6–78.6 cm) fork length, from Lac la Ronge, June to September, 1960.

Colour	Females	Males	Total	Percentage
1. Creamy white	70	66	136	40.4
2. Pale yellow	73	71	144	42.7
3. Yellow orange	18	28	46	13.6
4. Bright orange	3	8	11	3.3

Bright-fleshed fish ranged from 19 to 29 inches in length, thus no correlation with size was found. Although the two sets of colour standards cannot be accurately compared, it is apparent that Miller and Kennedy (1948) found a much higher percentage of trout with bright-coloured flesh in Great Bear Lake than is present in Lac la Ronge. The possible relation of flesh colour to spawning is referred to below in the discussion of spawning and egg diameter.

LIFE HISTORY

SPAWNING

The lake trout in Lac la Ronge usually spawn in the first week of October at depths of 1 to 3 metres (3–10 ft) on stony or rocky reefs. Since most of the lake is characterized by rocky shores and islands there is an abundance of bottom suitable for spawning. In several years lake trout eggs have been collected for hatchery purposes on reefs south of Bear Island in the north central part of the lake. These operations have made it possible to obtain detailed observations on the spawning trout.

The spawning run usually begins to come in on the reefs about September 25 but few ripe males or females are found before October 1. The males showed a slight tendency to precede the females in reaching the spawning area and becoming ready to spawn. In five years, the periods at which trout spawn was taken near Bear Island are as follows:

- 1949, October 3–9, a few eggs taken September 28
- 1950, October 4–11
- 1952, October 1–3
- 1953, October 2–6
- 1959, October 4–9

Thus the trout of Lac la Ronge appear to spawn in a well defined and rather short period which usually lies within the first week of October. Restriction of the spawning period to a week or less appears to be somewhat uncommon. In the Great Lakes, Van Oosten (1935) indicates spawning periods of more than one month. However, McCrimmon (1958) indicates that trout spawning in Lake

Simcoe, Ontario, was mostly completed in 7 to 9 days and Royce (1951) reports that in Lake George, New York, it is completed in 7 to 10 days. In the Great Lakes and in eastern Canada spawning is often in late October or November. In Great Slave Lake (latitude 62°) spawning takes place in mid-September and in Great Bear Lake (latitude 66°) spawning begins in mid-August (Miller and Kennedy, 1948). The number of spawning fish handled varied in the five years from 320 to 650. In four years in which records are available the males outnumbered the females, making up 66, 57, 58 and 55 percent, an average sex ratio of 1:0.7. In 1950, 1952, 1958 and 1959 the opportunity was taken to tag and release a considerable number of the trout captured on the spawning grounds.

Water temperatures of about 13° C (55.4° F) were common in late September when the trout began to arrive on the reefs. Spawning usually started at about 11° C (51.8° F) and at the end of the spawning period water temperatures of 9 to 10° C (48.2–50° F) were commonly observed. Spawning of lake trout in water temperatures of approximately 10 to 12° C (50–53.6° F) has been reported by many investigators. Royce (1951) reported that in some lakes in New York State, spawning occurs about the time of autumn circulation. McCrimmon (1958) also notes that lake trout in Lake Simcoe, Ontario, come to the spawning grounds at the time of the fall turnover. At Lac la Ronge the autumn turnover usually occurs in late August or early September. Thus the spawning temperatures referred to above for Lac la Ronge are not just surface temperatures but extend to the level of the spawning beds and deeper.

The age at which the trout of Lac la Ronge reach sexual maturity ranges from 5 to 8 or 9 years. A very few trout were mature at 5 years, nearly one-third at 6 years, two-thirds at 7 and almost all at 8. The correlation of length with sexual maturity was somewhat closer than that with age. Thus only the largest of the 6-year-olds were mature and any fish more than 20 inches (51 cm) in length and weighing more than 3 lb (1.4 kg) was almost certain to be mature although the age of a 20-inch trout might be anywhere from 5 to 9 years. Lake trout in the New York lakes (Royce, 1951) and in small lakes in Ontario (Martin, 1952) mature somewhat earlier. Those in Great Slave Lake mature a year or two later (Kennedy, 1954) and those in Great Bear Lake not until their 13th year when they are still only 16.5 inches (42 cm) long and 2 lb (0.9 kg) in weight (Miller and Kennedy, 1948).

The fork length distribution of the spawning run was determined from two samples, 145 measured in 1958 and 233 in 1959. Since both samples have the same range and mode they have been put together. The combined distribution arranged by mid-class lengths in inches is as follows:

Length	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
No. of trout	8	14	30	63	75	67	54	32	21	7	1	2	2	0	1	0	1

The modal length of 24 inches (61 cm) corresponds to the average length of an 8-year-old-trout. Reading the presumed ages of fish of other length from the growth curve (Fig. 3 below) it can be deduced that 74% of the spawning

run was made up of trout from 7 to 10 years of age and 82% from 7 to 12 years of age. Examination of the scales of a small sample of fish from the spawning run confirmed this deduction. They were from 7 to 12 years old with the largest number in the 8-year class.

It is known that the lake trout in some northern waters do not spawn every year. Thus trout in Great Bear Lake spawn about once in three years (Miller and Kennedy, 1948), those in Great Slave Lake usually in alternate years (Kennedy, 1954). Cuerrier and Schultz (1957) suggest that the lake trout of Waterton Lake, in southwestern Alberta, spawn in alternate years up to 10 years and annually thereafter. Observations at Lac la Ronge suggested that some of the mature female trout did not spawn every year. Samples of trout ovaries were taken from June to September, 1960, to determine the rate of egg growth. From each trout a sample of about 5 cc of eggs was taken, together with date, locality and fork length. Flesh colour was recorded for 164 of the 228 fish examined. The egg samples were preserved in 10% formalin for later measurement.

The average diameter of formalin-hardened trout eggs increased from 2.8 mm in late June to 6.1 mm at spawning time, October 5 and 6. The following averages are based on the measurement of 228 samples, a sample being 10 eggs from each fish. In the period August 16 to 31 the samples were too few to justify calculation.

June 20-30 average	2.8 mm	August 1-15 average	4.7 mm
July 1-15	" 3.5 mm	September 1-15 average	5.8 mm
July 15-30	" 4.1 mm	October 5-6 (spawning)	6.1 mm

These egg sizes are not unlike those reported by Dymond (1928) who found that in late August, 1927, the larger lake trout in western Lake Ontario had eggs from 4 to 5 mm in diameter.

Among the 228 female trout from which samples were taken, 18 had "under-sized" eggs. These ranged from 1.6 to 2.5 mm diameter and were never more than 60% of the average diameter of "normal" eggs taken on the same date. These fish ranged from 20 to 31 inches in length and were apparently sexually mature but not preparing to spawn in the current season. This group of non-spawners represents only 8% of the sample, a much smaller proportion than those mentioned above for trout in Great Slave and Great Bear Lakes. Of these 18 non-spawners 7 had bright flesh colour, a marked contrast with the spawning females, almost all of which were pale. Miller and Kennedy (1948) found an even higher proportion of bright-fleshed individuals in the non-spawning trout of Great Slave Lake.

RATE OF GROWTH

Information for the growth study comes from the scales of more than 900 trout for which fork length, weight and sex were also recorded. Most of these fish were taken in "standard" gangs of gill net described in a later section. A large sample was taken in the first 2 years of investigation, 1948 to 1949, and a

second large sample 10 years later, in 1958. The distribution of these samples was as follows:

	Main lake	Hunter Bay
1948	178	22
1949	109	123
1953	43	59
1958	277	113
Totals	607	317

Three or more scales from each fish were impressed on cellulose acetate slides with a jeweller's roller and read by projection at a suitable magnification. Most of the scales were examined independently by two experienced readers who agreed on about 90% of the interpretations. Twelve of the 924 readings have been rejected as representing distinctly abnormal conditions. Helpful advice on scale interpretation was received from the experienced readers trained by Dr W. A. Kennedy of the Fisheries Research Board of Canada Biological Station, London, Ont.

The growth analysis of the Lac la Ronge trout was designed to determine the general growth rate and whether there was (a) any sex difference, (b) any difference between growth of trout in Hunter Bay and the main lake, (c) any change in growth rate over the 10-year period of study.

By determining separate average lengths for males and females of each age group and plotting these as two curves it was shown that there was no detectable difference in the growth rate of the two sexes. This was true for the whole samples from the main lake and from Hunter Bay and also for the largest sub-sample of 277 trout from the main lake, in 1958.

A comparison was made of the average lengths of trout of each age group from the main lake in 1948-49 and those taken in 1958. The average lengths of the 1958 fish were consistently greater than those of 1948-49. In the year-classes 7 to 11, in which sample numbers ranged from 52 to 108, the comparable average lengths are as follows:

	1948-49	1958
7 years	22.9	23.4
8 years	23.7	24.4
9 years	24.9	25.8
10 years	25.7	26.5
11 years	26.9	27.6

Since the trout caught in 1958 in the main part of Lac la Ronge averaged nearly 3% longer than those caught in 1948-49 it would appear that a slight increase in rate of growth may have occurred in this period. The sample is not large enough to place great reliance on this determination. A similar analysis of the trout caught in Hunter Bay showed no evidence of change in the rate of growth over the 10-year period.

A preliminary examination revealed a difference in the growth pattern of trout in the main part of Lac la Ronge and in Hunter Bay. Thus the age and length data for trout from the two areas are shown separately in Tables II and III and two curves appear on the graph Fig. 3. An impressive feature of these data

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[illegible]

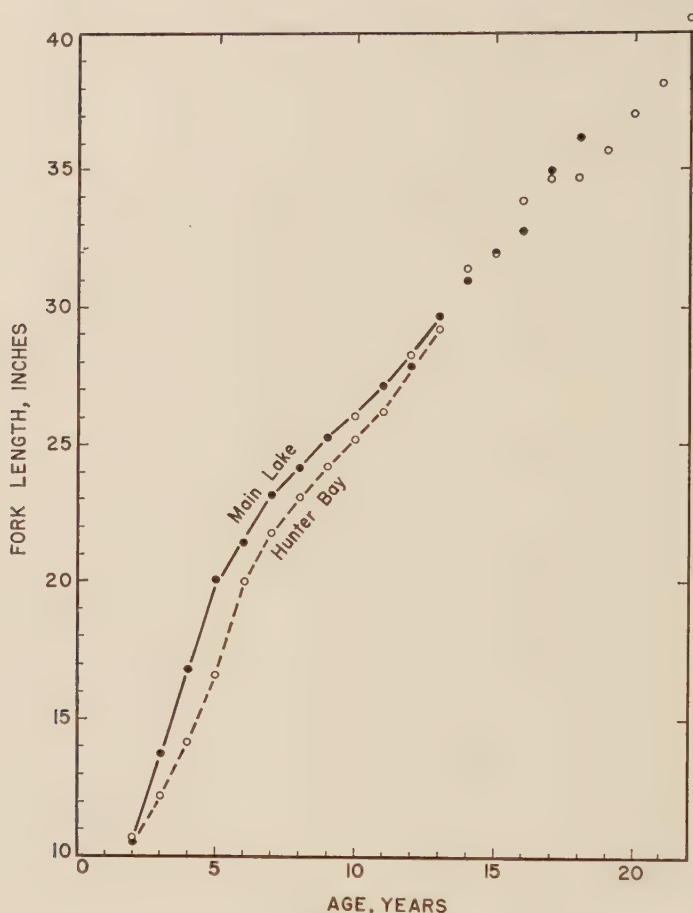


FIG. 3. Average growth in length of lake trout in the main lake and in Hunter Bay, Lac la Ronge.

is the wide variation in growth rate of individual fish. Examination of Table II shows that a fish in its 6th year may range from 13.5 to 26.0 inches, one in its 10th year from 20 to 30.5 inches, and one in its 13th year from 26 to 34 inches. Kennedy (1954) found even greater diversity in the very large samples of trout from Great Slave Lake.

The average rates of growth in trout from the main lake and Hunter Bay are indicated in Fig. 3. The points plotted are the averages shown at the bottom of the columns in Tables II and III. Thus the curve for the main lake is based on a sample of 601 and that for Hunter Bay on 311 trout. It is apparent that trout in the main lake grow fairly rapidly for the first 5 years then begin to slow down. Those in Hunter Bay grow more slowly in the first 4 years then increase and continue steadily to 12 or 13 years at which time they have "caught up" with those in the main lake. Both groups grow at similar rates in the later years as

far as can be determined from the relatively small samples of these very large and old trout. The maximum divergence between the two populations is at 5 years where the average trout in the main lake is 20.1 inches long and weighs 3.5 lb while an average 5-year trout in Hunter Bay is 16.6 inches long and weighs 1.5 lb. It is suggested that young trout in the main lake grow faster because of warmer water and richer food supply but that after the age of 5 years some change in feeding may take place which reverses the advantage and allows the Hunter Bay trout to grow faster and eventually to overtake those of the main lake at the age of about 13 years. An alternative or additional explanation lies in the degree of mixing or exchange of trout between the two areas, suggested by tagging results described below. If substantial mixing occurs, the fast-growing individuals from the main lake might raise the apparent rate in Hunter Bay and slow growing individuals from Hunter Bay might lower the apparent rate of growth of trout in the main lake.

The difference in growth rate between the trout of the main lake and Hunter Bay provides a very interesting parallel with the situation demonstrated by Kennedy (1954) in Great Slave Lake. The western part of Great Slave Lake is shallower, warmer and generally less productive than the eastern part. Trout from the warmer western part grew considerably faster than those from the east (Kennedy's figure 3A, p. 839) especially up to 15 years. From 15 to 19 years the rate of growth of trout in the eastern part of the lake was considerably faster than that in the west.

Various authors have compared the rate of growth of lake trout in different areas, referring to faster growth near the southern limits of its distribution and slower in the far north. Very rapid growth has been reported in the Finger Lakes of New York State by Royce (MS, 1943) and in the Waterton Lakes in southwestern Alberta by Cuerrier and Schultz (1957). Fast growth was also found in Lake Opeongo and other small lakes of Algonquin Park, Ontario, by Fry and Kennedy (1937) and Martin (1952). Intermediate to slow growth has been found in large lakes of northern Saskatchewan (Rawson, 1959) and in Great Slave Lake (Kennedy, 1954). The slowest growth reported for lake trout appears to be that in Great Bear Lake (Miller and Kennedy, 1948). The rate of growth of trout in Lac la Ronge, as indicated in Fig. 3, is very close to that in Cree and Wollaston Lakes (Rawson, 1959) and intermediate between the rates shown by Kennedy (1954) for the east and west part of Great Slave Lake. It is also similar to that recorded for trout in Lake Michigan by Cable (1956).

The relation of length to weight of the Lac la Ronge trout was determined by plotting the lengths and weights of most of the specimens recorded in Tables II and III and drawing the best curve. The result was verified by averaging the weights of all individuals falling in certain length classes. No significant differences were found in the length-weight relationship of males and females nor between trout from the main lake and Hunter Bay. The results are presented in Table IV. While the young trout are about the same weight as those of similar lengths in Great Slave (Kennedy, 1954, table 1) the old trout (over 15 years) in Lac la Ronge become 25 to 50% heavier.

TABLE IV. Average fork length and average weight in pounds of lake trout in Lac la Ronge.

Inches	Pounds	Inches	Pounds	Inches	Pounds	Inches	Pounds
7	0.10	16	1.41	25	7.2	34	20.5
8	0.16	17	1.78	26	8.2	35	22.5
9	0.28	18	2.1	27	9.2	36	25.0
10	0.41	19	2.6	28	10.4	37	27.0
11	0.55	20	3.4	29	11.8	38	30.0
12	0.68	21	4.1	30	13.2	39	32.0
13	0.84	22	4.8	31	14.9	40	35.0
14	1.02	23	5.6	32	16.8	41	38.0
15	1.21	24	6.3	33	18.8	42	40.5

Only a small percentage of the trout in Lac la Ronge survive past their 19th year, at which time the average length is about 36 inches (91 cm) and the average weight about 25 lb (11.2 kg). The largest for which we have a scale sample was 40.5 inches (101 cm) in length, weighed 34.5 lb (15.6 kg) and its age was interpreted as 23 years. Lake trout weighing 30 lb or more are naturally of tremendous interest to the angler, and although they represent only a small fraction of the population they are by no means rare. Some of the lengths and weights of large trout taken in Lac la Ronge during the last 10 years are recorded in Table V. Only those measured and weighed by fisheries research personnel or officers of the Department of Natural Resources are included. More than

TABLE V. Fork lengths and weights of some very large trout caught in Lac la Ronge.

	Inches	Pounds		Inches	Pounds
1949	38.0	37.2	1956 (cont'd)	38.5	32.5
	38.5	32.5		40.0	37.3
1950	37.7	30.5	1957	38.0	32.0
	38.5	34.5		42.0	33.0
	40.5	32.0	1958	39.0	35.0
1951	40.0	34.0		41.0	32.0
	40.5	34.5	1959	38.0	33.1
1952	41.0	37.0		38.5	36.0
				40.5	33.7
1953	39.5	36.2		42.2	37.5
	40.5	34.5		47.0	37.0
	42.0	41.0		48.1	43.0
1954	39.5	32.5	1960	34.5	30.5
1955	40.5	28.5		38.5	32.5
	41.0	28.5		40.5	38.5
1956				42.0	34.0
	36.5	36.2		46.0	41.5
	38.0	32.5			

half of these very large trout were caught in Hunter Bay or in the Narrows which joins Hunter Bay with the main part of Lac la Ronge. In 9 of the 11 years represented in Table V, a trout from Lac la Ronge was the largest caught in Saskatchewan.

FOOD

The stomach contents of all trout taken in sampling were examined and recorded in the field but any material not readily identified was preserved for laboratory analysis. Of 511 stomachs examined 257 were empty. The younger fish took somewhat different food than the older ones, so the two groups have been considered separately. The first is made up of those with fork lengths up to 16 inches (40.6 cm), which includes all of the 2-year trout, most of the 3-year-olds and a few 4-year-olds.

Forty-two trout from 7 to 16 inches (17.7–40.6 cm) fork length were obtained in the course of the investigation. Nineteen of these were empty and the stomach contents of the remaining 23 are recorded in Table VI. The main invertebrate food was *Mysis relicta*, followed by moderate numbers, but little volume, of *Pontoporeia affinis* and Entomostraca. The fish eaten included mainly

TABLE VI. The food of 23 small trout 7–16 inches (18–41 cm) in fork length in Lac la Ronge; the stomachs of 19 additional trout were empty.

	Percentage frequency of food item in stomachs	Estimated percentage of total volume of food
<i>Mysis</i>	25	17
<i>Pontoporeia</i>	14	2
Entomostraca	9	+
Chironomid larvae and pupae	14	+
Ciscoes	9	31
Sculpins	17	21
Ninespined sticklebacks	26	18
Unidentified fish	16	9

ciscoes, *Leucichthys zenithicus* and *L. tullibee*, ninespine sticklebacks, *Pungitius pungitius*, and sculpins. Of 17 sculpins taken from the trout stomachs 9 were deepwater sculpins, *Trigloopsis thompsoni*, and one was *Cottus cognatus*. *Mysis* was particularly numerous in the stomachs of 2-year-old fish (7 to 12 inches) and is undoubtedly a very important food of young trout in Lac la Ronge, as it is in Lake Superior (Eschmeyer, 1956), Great Slave Lake (Rawson, 1951), Keuka Lake, New York (Royce, 1951) and elsewhere. The deepwater sculpin is apparently one of the first fish of suitable size and in suitable location to provide food for young trout. The frequent feeding on ninespine sticklebacks suggest that this species is also common in the deep water. Ciscoes, although a main food of the larger trout, were found in only two trout under 16 inches.

The food of larger trout, 16 to 40 inches (40.6–101) fork length, is summarized in Table VII. This represents the examination of the 469 stomachs, 231 containing food. The fish items make up 90% of the food occurrences and invertebrates barely 10%. The fish eaten include 10 of the 19 species recorded for the lake (Rawson and Atton, 1953) but only the first 6 listed in Table VII

TABLE VII. Occurrence of food items in stomachs of 231 large lake trout from Lac la Ronge; 238 additional stomachs were empty.

Food items	Number of stomachs	Percentage frequency
Unidentified fish remains	132	57.1
Ciscoes, <i>Leucichthys</i> spp.	53	22.9
Whitefish, <i>Coregonus clupeaformis</i>	13	5.6
Ninespine stickleback, <i>Pungitius pungitius</i>	13	5.6
Longnose sucker, <i>Catostomus catostomus</i>	5	2.2
Yellow perch, <i>Perca flavescens</i>	5	2.2
Sculpins, <i>Triglopsis</i> and <i>Cottus</i>	5	2.2
Burbot, <i>Lota maculosa</i>	2	0.87
Walleye, <i>Stizostedion vitreum</i>	2	0.87
Spottail minnow, <i>Notropis hudsonius</i>	2	0.87
Lake trout, <i>Cristivomer namaycush</i>	1	0.43
<i>Mysis relicta</i>	16	6.93
<i>Pontoporeia affinis</i>	3	1.29
Mayfly nymphs	2	0.87
Stonefly nymphs	1	0.43
Winged ants	2	0.87

appear in significant quantities. The ciscoes are clearly the main food of adult trout in Lac la Ronge. *Mysis* is the only invertebrate food of common occurrence. The volumes of the individual food items in trout stomachs were not measured. However, considering the relative size of the food organisms and the average numbers found in individual trout stomachs, it is possible to make a rough estimate of the contribution of different items. Ciscoes probably provide about 50% of the food of large trout, whitefish about 15% and all other fish about 30%. The invertebrates, although of frequent occurrence, are small in size and probably provide less than 5% by volume of food of these trout.

In two other lakes of northern Saskatchewan, Cree and Wollaston (Rawson, 1959), fish provide 95% and 85% of trout food by volume, with ciscoes the most important species followed by whitefish, suckers and other species. In Great Slave Lake ciscoes were also the major trout food, followed by cottids, burbot, whitefish and longnose suckers, and with *Mysis* again the main invertebrate food (Rawson, 1951). Trout in Lake Athabaska had a similar diet (Rawson, 1947). In Lake Nipigon, Ontario, Clemens *et al.* (1924) report ciscoes as the main food followed by sticklebacks, cottids, suckers and whitefish. McCrimmon (1956) records the cisco as the main food of trout in Lake Simcoe, Ontario. It is clear that in most of the large lakes in Canada, the larger lake trout feed mainly on fish and especially on ciscoes. In small lakes, such as those of the Algonquin

Park, Ontario, plankton and surface and bottom insect foods are taken in large amounts (Ricker, 1932; Martin, 1952). In small lakes of the Northwest Territories the lake trout had eaten mostly fish but insects were found in nearly half the stomachs and molluscs and crustaceans in a few (G. Hunter, Fisheries Research Board of Canada, Arctic Unit, personal communication).

In the deeper water of Lac la Ronge where the lake trout is the dominant piscivore, the burbot is probably its main competitor, eating considerable quantities of ciscoes. In the main lake where, judging from our standard net sets the burbot is more abundant than the lake trout, this competition may have an important effect on trout production. In Hunter Bay, where trout appear to outnumber burbot by about 3 to 1, the competition would have less significance. Pike and walleyes also feed extensively on several of the fish species which are eaten by the trout. This competition would be most active in the spring and fall when the trout come into shallow water.

PARASITES

Internal parasites were collected from the lake trout and additional specimens were recovered from the preserved stomach contents. We are indebted to Dr Betty-June Myers, Institute of Parasitology, Macdonald College, for identification of these materials.

Cestodes collected from the alimentary canal were mostly *Eubothrium* (probably *salvelini*) with smaller numbers of *Proteocephalus* sp. A few cysts of the cestode *Triaenophorus crassus* were found in the flesh. This parasite is widespread in the trout of northern Saskatchewan and the Northwest Territories but apparently not numerous except in a few lakes, mostly of small size.

Unidentified nematodes, mostly larval, were found in the intestine and occasionally in the swim bladders of the trout. Nematodes in the swim bladders of 4 lake trout from Little Bear Lake, 40 miles south of Lac la Ronge, were identified as *Cystidicola stigmatura* by Dr R. C. Anderson, Ontario Research Foundation, Toronto.

An external copepod parasite, *Salmincola siscowet*, was frequently found attached to the body surface, usually on the fins. We are indebted to Dr Paul Illg, University of Washington, for this identification.

THE DISTRIBUTION OF TROUT IN LAC LA RONGE

It is well known that the distribution of trout in the lake is by no means uniform at any season nor the same in different seasons. In a general way trout movements are understood to be related to seasonal changes in temperature and to such vital activities as feeding and spawning. It is of special biological interest to determine the effects of temperature more exactly and to follow the seasonal movements of the trout population. Such information is of course vital to the success of the angler, the commercial fisherman and to the administrator concerned with utilization and protection of fish stocks.

The primary source of information concerning trout distribution has been systematic gill netting throughout several summers and in all parts of the lake. Depths, temperatures and feeding activities were recorded for each set. Tagging and recovery have provided important information on the movements of individual trout. Spawn-taking operations in 5 years have made it possible to examine large samples of mature trout and to tag many of them. Forty years of records of commercial fishing, both summer and winter, and interviews with experienced fishermen have helped to complete the picture, especially concerning winter distribution.

SEASONAL DISTRIBUTION IN RELATION TO DEPTH AND TEMPERATURE

Gill nets used in sampling the lake trout population were in the form of standard gangs 300 yards (275 m) in length and made up from six 50-yard lengths of $1\frac{1}{2}$ -, 2-, 3-, 4- and $5\frac{1}{2}$ -inch stretched mesh. These were set along the lake bottom for overnight periods averaging about 22 hours. Uniform specifications and techniques of setting were maintained throughout the 10-year period, with one important exception. In the first 4 years, from 1948 to 1952, cotton and linen nets were used but from 1953 to 1959 nylon nets were always used. In 1958 and 1959 the netting program was planned specifically for the trout investigation. Thus care was taken that in every 2-week period nets were set in all depth ranges and in different areas of the lake. The catch from each mesh size was separated and depths were measured at each end and in the centre of the net so the depth at which each trout was caught could be recorded. At each set a vertical series of temperatures was taken at 1-metre intervals with an electrical resistance thermometer.

The depth distribution of trout in Lac la Ronge in the summers of 1958 and 1959 is presented in Fig. 4. Isotherms in degrees Centigrade at 2-degree intervals have been plotted for the periods May to September. Lac la Ronge is a very large lake with a northern islands region and a southern open area. Thermal stratification is relatively stable in deep basins between the islands at the north and rather unstable in the exposed southern area. (Atton, MS, 1955b). Thus a set of isotherms for the whole lake can indicate only the generalized condition for the whole area. Temperature series at individual stations during late July and August, 1958, showed sharp thermoclines with as much as 7°C drop in temperature in 5 m. Autumn circulation usually occurs first in the open water (about Sept. 9 in 1952), a little later in the islands area (Sept. 12, 1952) and still later in Hunter Bay. Superimposed on the isotherms are vertical polygons representing the total numbers of trout caught in each 5-metre depth unit over a half-month period. These polygons represent the sum of the catch in the half-month period from the number of sets made in this period. Thus they do not represent equal fishing efforts.

The upper chart in Fig. 4 represents the season of 1958. The breakup of ice was completed on May 11 and observations began on May 20. In the remainder of May trout were caught in all depths from 5 to 35 m with the greatest number

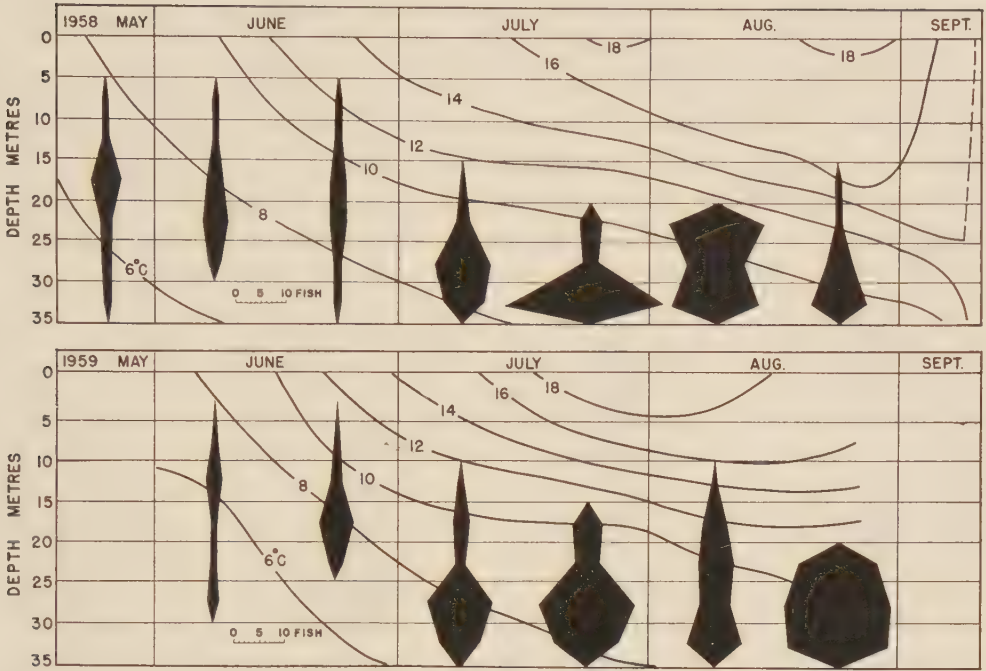


FIG. 4. Charts showing the vertical distribution of lake trout caught by gill nets in relation to the water temperatures through the summers of 1958 and 1959, Lac la Ronge.

between 15 and 20 m. Surface temperatures increased from 6.7 to 9.6 and bottom from 5.5 to 6.2°C. In the two halves of June, trout continued to be caught in almost all depths and with no great concentration at any level. However, by July 1 the surface water had warmed beyond 14° and the 10° isotherm had dropped below 15 m. In the first two weeks of July no trout were caught above the 15-metre level and the maximum catch was between 25 and 30 m where temperatures were mostly between 8 and 9°C. In the second half of July and throughout August, as the thermal stratification became more pronounced, very few trout were caught above 20 m. Thermal stratification was destroyed in early September in the open lake and a little later among the islands. Although no test netting was possible at this time in 1958, it is known that trout came up into shallow water where they were taken in large numbers by anglers casting at the surface.

In 1959 the ice remained on Lac la Ronge until May 27 and thermal events were nearly 2 weeks behind those of 1958, throughout the summer (Fig. 4). Lake trout were caught fairly uniformly at most depths throughout June. In the first half of July the 10° isotherm had gone down to 15 m and the trout were beginning to concentrate in the deep water, 25 to 35 m. In the last half of July this deep concentration was still greater. Because of the late season the depth of heating in 1959 was not as great as that in 1958 and the 10° isotherm barely reached the 25-metre level. However, the surface water was warmer in 1959

and thus the “thermocline” was more sharply defined than in 1958 (a range of 6° in about 14 m in August, 1958, and 6° in 10 m in August, 1959).

Hunter Bay, about 30 miles from laboratory headquarters, was sampled less often than the main lake. However, in 1958 sufficient data to demonstrate the vertical distribution of trout with temperature were obtained for one-half of June, July, August and September (Fig. 5). In the first half of June, with

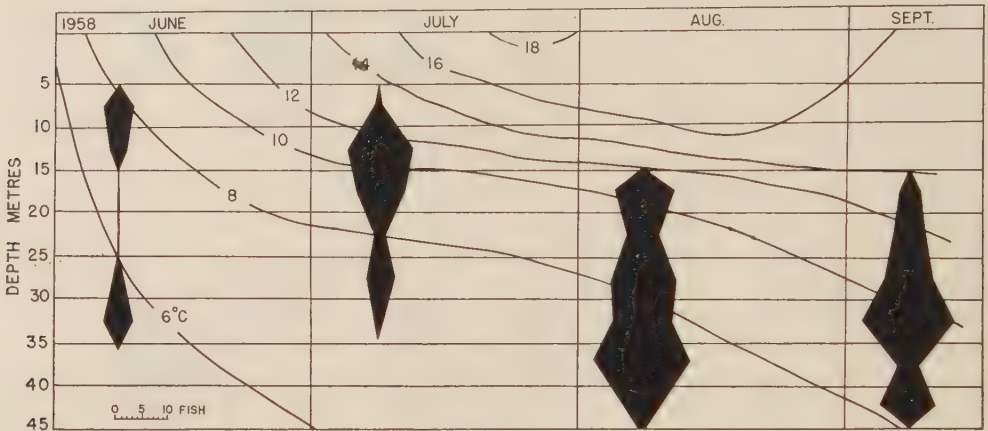


FIG. 5. Chart showing the vertical distribution of lake trout in relation to water temperatures in Hunter Bay, Lac la Ronge, 1958.

bottom temperatures about 6° and surface 8.5°, trout were caught in about equal numbers in shallow (5–15 m) and deep (25–35 m) waters. In early July, while thermal stratification was beginning, considerable numbers of trout were still caught between 10 and 30 m. In the first half of August no trout were caught above 15 m but considerable numbers at all depths from 15 to 45 m. A similar situation was observed in the first week of September. As in the main lake 1948 and 1949 (Fig. 4) trout were mostly caught below the 10° isotherm—a few between 10 and 12° and very few between 12° and 14°.

Having measured the temperature at net level for every gill net in 1958 and 1959 it was possible to tabulate the distribution of the trout caught by temperature as follows:

Temperature class, °C ²	5	6	7	8	9	10	11	12	13	14
No. of trout caught	5	39	29	171	147	111	3	3	0	1

Thus of 519 trout caught in the two seasons only 1.35% were from water warmer than 11°C and 22.7% from water warmer than 10°C. It can be inferred that the trout in Lac la Ronge prefer temperatures of less than 10°C (50°F). Ferguson (1958) in an extensive study of preferred temperatures of freshwater fish records 12°C as the upper limit of preferred temperature for the lake trout.

²Temperatures were read to the nearest tenth-degree; the class 5 includes readings from 5.0° to 5.9°, etc.

In order to remain in water cooler than 10° or 12°C the trout move down in July and August to depths of at least 15 and usually 20 m (Fig. 1). In Hunter Bay where nearly one-half its area is deeper than 20 m this will not necessitate much horizontal movement. In the main lake, however, about 85% of the water area is less than 20 m deep so the trout, to remain in cool water, must move into the restricted deeper areas. The resulting concentration of trout in the deep "holes" is most fortunate for the anglers who continue to catch trout effectively in these regions during July and August.

MOVEMENTS OF TROUT AS INDICATED BY TAGGING AND RECOVERY

Lake trout were first tagged in Lac la Ronge in 1950. A few were tagged in 1952 and larger numbers in 1958 and 1959. Specimens for tagging were selected from the gill-net catch, taking only those which were active and showed no signs of damage from the nets. In 1950, 1952 and 1958 Petersen type tags with half-inch diameter plastic discs were used. These were attached with monel metal pins just below the dorsal fin. In 1959 a button-type tag was used attached to the operculum by means of special pliers as described by Cable (1950). Tags were returned from fish caught by anglers and from gill nets set by domestic fishermen, our own standard gangs and especially from those used by hatchery personnel to obtain trout for spawn taking.

Returns from 429 trout bearing Petersen tags numbered 60, or 14%. From 322 marked with button-type tags only 1 was recovered. The reason for this discrepancy is not known.

A summary of the trout tagged with Petersen tags and the recoveries to December, 1960, is presented in Table VIII. Those tagged throughout the summers of 1952, 1958 and 1959 were taken in our experimental nets in all parts of the lake. Those at the spawn camp were tagged in late September or early October at a point about 2 miles south of Bear Island, Fig. 6.

The maximum distance from the point of tagging to the place of recovery was 22 miles. Nine trout were recovered from 15 to 22 miles from the point of tagging, 12 at distances 4 to 14 miles and 8 at distances of 1 to 4 miles. The average distance for these 29 trout was 8.8 miles. Another 31 trout, tagged at the spawn camp, were recovered within a mile of the point of tagging in the years which followed.

The time from tagging to recovery of lake trout in Lac la Ronge has varied from one month to nearly 3 years. Approximately 12% were recaptured in the calendar year in which they were tagged, 60% in the second year and 28% in the third year.

The locations of tagging and recapture of 24 trout which were caught at some distance from the site of tagging, are indicated in the sketch map, Fig. 6. Thirty-six other trout, which had travelled only short distances, have not been

TABLE VIII. Recovery of lake trout marked with Petersen type tags in Lac la Ronge, 1950, 1952 and 1958. (Of 123 tagged during summers, 15.4% were recovered; of 306 tagged at spawning, 13.4% were recovered.)

	1950			1952	1958			All years
	Summer	Spawning	Total	Summer	Summer	Spawning	Total	
Number of trout tagged	56	131	187	28	67	147	214	429
Recoveries, angling								
Same year	2	0	...	0	2	0	...	
Next year	2	2	...	4	2	3	...	
Third year	0	2	...	0	2	2	...	
All years	4	4	8	4	6	5	11	23
Recoveries, domestic and experimental nets								
Same year	2	0	...	0	0	0	...	
Next year	1	2	...	0	1	0	...	
Third year	0	0	...	0	3	1	...	
All years	3	2	5	0	4	1	5	10
Recoveries, nets at spawning								
Same year	1	0	...	0	0	0	...	
Next year	0	0	...	0	1	18	...	
Third year	0	5	...	0	0	2	...	
All years	1	5	6	0	1	20	21	27
Total recoveries	...	...	19	4	...	...	37	60
% recovered	...	...	10.2	14.3	...	...	17.3	14.0

plotted. Trout tagged in the spawn camp area south of Bear Island have been recaptured in such remote areas as Pickerel Bay (in the southeast part of Hunter Bay), Fox Point on the south shore, south of the La Ronge townsite, off the inlet of the Nemeiben River, and in Four Portages and Pipestone Bay at the north. A trout tagged near Hunter Narrows has crossed the lake to Nut Point on the west and one tagged south of Nut Point went northeast into Four Portages Bay. Of particular interest is the interchange of trout between the main lake and Hunter Bay. Two trout tagged in Hunter Bay were recaptured some 15 miles west at Big Island and Bear Island respectively. Three trout tagged in the main lake were recaptured in Hunter Bay. Thus 5 of a total of 60 recaptures have passed through Hunter Narrows suggesting that a moderate rate of exchange occurs between the two populations. If this rate applies to all trout randomly and continues over a period of 5 to 10 years, the resulting mixture of the two populations may account for part of the apparent convergence of growth rates shown for the two areas in Fig. 3.

In the years 1950 and 1958, 278 trout were tagged on the spawning grounds. From this group 25 have been recovered in spawning runs 1 and 2 years later

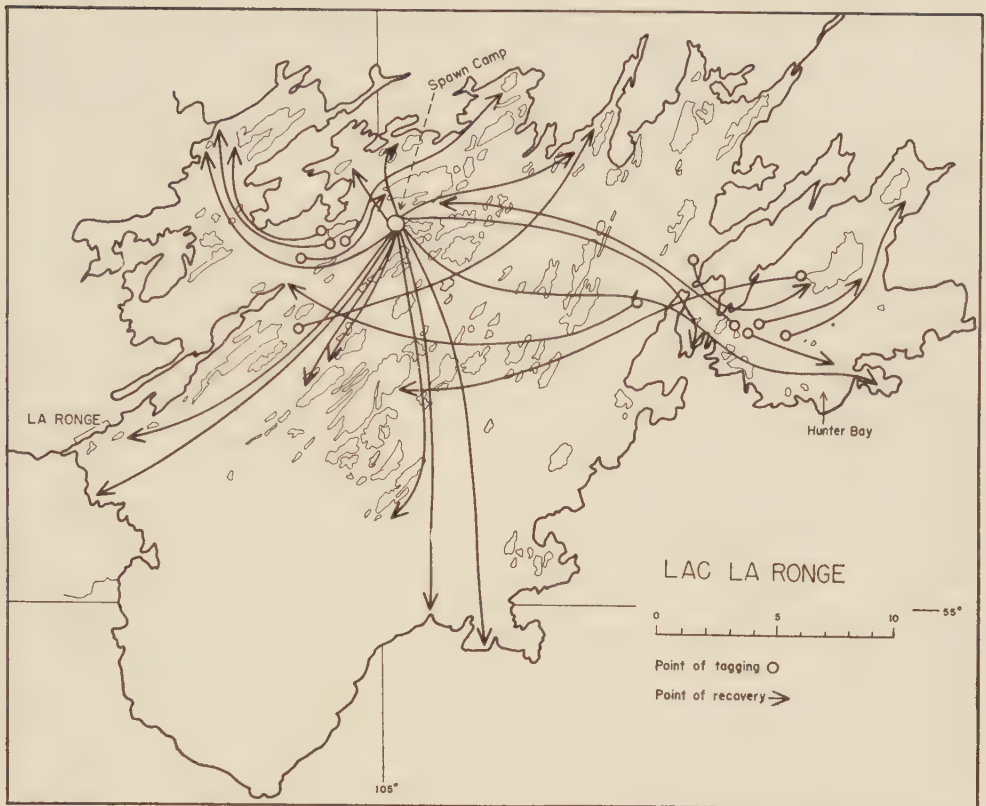


Fig. 6. Location of tagging and recovery for 24 lake trout in Lac la Ronge. Note that 30 other trout were recaptured a short distance from their place of tagging.

at the same location, and 12 have been recovered elsewhere in the lake at various seasons. This result suggests a considerable degree of "homing" of trout to the same spawning grounds. Unfortunately, it has not been possible to carry on autumn sampling on other spawning grounds to test the degree of mixing of different runs. Homing of lake trout has been demonstrated by Martin (1960) in small lakes of the Algonquin Park, but McCrimmon (1958) found no evidence of homing in tagging studies in Lake Simcoe, Ontario.

OTHER INFORMATION CONCERNING THE DISTRIBUTION OF TROUT

The spawning run has been referred to above in the discussion of life history. Since there are many known spawning grounds in different parts of the lake it is unlikely that trout from any area would need to move more than 2 or 3 miles to spawn. In terms of population movements, it should be noted that the spawning migration would not affect the large group of trout less than about 23 inches length and 7 years of age. It is probable also that about two-thirds of the mature

trout in Lac la Ronge spawn in any one year, thus one-third of the mature trout might not migrate at spawning time.

Careful analysis of the food taken by lake trout and their association with other species of fish in the gill nets failed to provide any evidence of daily or seasonal migrations of trout for feeding purposes. Since the ciscoes are the main food of trout the association of these two species was examined. Trout were very frequently caught in the small mesh nets when attempting to eat small ciscoes already gilled in the twine. However, in net catches where ciscoes were particularly abundant (more than 100 per set) lake trout were usually few and often were absent. It would seem that the various fish on which the lake trout feed in Lac la Ronge are sufficiently abundant that the trout do not need to make any special feeding migrations. This may be contrasted with lakes in the Algonquin Park, Ontario, where Fry (1939) and Martin (1952) have shown that lake trout may come up through the thermocline to feed on yellow perch which are concentrated in the warmer water.

The field program for this study did not include netting for trout beneath the ice. However, extensive commercial netting in the winters from 1922 to 1945 took an average of more than 100,000 lb of trout per year. Careful questioning and comparison of statements from several commercial fishermen who took part in these operations have provided useful information concerning winter distribution of the lake trout. The winter fishing began on December 1 about 10 days after the ice covered the lake. Gill nets were usually $5\frac{1}{2}$ inch stretched mesh, 36 meshes high and about 17 feet (5.2 m) in height. These were set at first in 30 to 60 feet (9 to 18 m), sometimes fairly close to shore. In January and February the trout tended to move offshore and somewhat deeper but nets were rarely set in more than 80 feet (24 m) of water. Trout could be caught in all parts of the lake, but about five main fishing areas were used. The western part of the open water was fished from Birch Island 3 miles south of Potato Point. A northwestern area was fished from camps on Nut Point, Freeman Island and Moose Point. The centre island group had camps on Brooks and Big Islands and south to Meraste Point. A fourth major fishing ground was in Hunter Narrows and Trout Narrows, 3 miles to the south. The fifth main camp was in Hunter Bay on Rainy Island. With the exception of the Birch Island region these are all still considered trout grounds. It is of interest that very heavy trout catches were made in this area of moderate depth near Birch Island in 1921 and 1922 and again for several years following 1940.

In summary, movements in response to water temperature are the main factor in explaining the seasonal distribution of trout in Lac la Ronge. The spawning migration brings most of the larger fish into shallow water at the beginning of October. Tagging has demonstrated rather extensive wandering of perhaps one-third of the population and exchange between the main lake and Hunter Bay of perhaps one-tenth. When the ice breaks many trout come into shallow water and remain there until warming forces them to move down. In July when thermal stratification is well established, the trout are at least 15 m down and in August, below 20 m (Fig. 1). They thus remain in water cooler than

12° and usually below 10°C. In September, when the surface water cools and autumn circulation occurs, the trout again come into shallow water. Even after the spawning period, trout can be caught in shallow water. Evidence from commercial fishing indicates that they are in moderate depths in early winter and tend to be widely dispersed during later months of ice cover.

POPULATION DATA

Information as to the abundance of lake trout in Lac la Ronge has been obtained by extensive use of standard gangs of gill net and less directly from the creel census and records of commercial catch. The catches in standard gangs provide some measure of the availability of trout more than 2 or 3 years of age. They also provide materials from which size distribution, year-class composition and rate of growth has been determined. Our limited program of tagging and recovery was designed simply to follow movements of fish and the results are not considered suitable for making estimates of the population of trout in the lake.

A summary of gill net catches in Lac la Ronge is presented in Table IX. These include 169 catches made in 1948, 1949, 1958 and 1959, in the main lake and in Hunter Bay. Hunter Bay is separated because it differs from the main lake in depth, temperatures, trophic condition and fish population. Gill netting in the period 1950 to 1957 was concentrated in certain areas and depths for the study of whitefish, walleyes (pickerel) and for other purposes. Thus the catch data for these years were not comparable to those in Table IX and are not included.

The general composition of the fish population in Lac la Ronge is suggested by the data in Table IX. Whitefish usually make up 40 to 50% of the catch numerically, ciscoes 30 to 40%. Two species of suckers contribute about 10%

TABLE IX. Summary of average numerical composition and total weight of gill-net catches in Lac la Ronge proper and Hunter Bay 1948, 1949, 1958 and 1959.

Number of gill-net sets	Main lake						Hunter Bay			
	1948-49 53		1958 41		1959 38		1948-49 15		1958 22	
	no.	%	no.	%	no.	%	no.	%	no.	%
Whitefish	64.2	40.3	72.2	39.2	79.7	42.6	57.7	60.6	59.1	53.2
Cisco	67.8	42.5	77.5	42.1	68.7	36.6	22.1	23.2	32.6	29.5
Longnose sucker	11.5	7.2	18.3	9.9	22.9	12.2	1.5	1.6	5.5	5.0
White sucker	5.1	3.2	0.56	0.38	1.4	0.76	0.9	1.0	2.5	2.2
Lake trout	1.9	1.2	3.9	2.0	4.9	2.6	4.6	4.8	7.9	7.1
Pike	2.2	1.4	0.88	0.47	0.81	0.44	2.3	2.4	0	0
Walleye (pickerel)	1.6	1.0	1.0	0.52	0.81	0.44	4.7	4.9	1.0	0.9
Burbot	2.0	1.2	9.0	4.9	7.8	4.3	1.4	1.5	1.6	1.48
Perch	3.2	2.0	1.2	0.6	0.31	0.17	0	0	0	0
All species number	159.5	...	184.5	...	187.3	...	95.2	...	110.2	...
Approx. av. weight per set pounds	152.	...	177.	...	180.	...	126.	...	151.	...
Kilograms	69.0		80.2		81.6		57.1		68.5	

in the main lake but much less in Hunter Bay. The lake trout follows these with about 2% by numbers in the main lake and 5% in Hunter Bay. Because of their large average size the lake trout represent nearly 12% by weight of the catch in the main lake and about 26% by weight of the catch in Hunter Bay.

Since the lake trout depends mainly on plankton-feeding and bottom-feeding fish for its food, the ratio of trout and other piscivores to non-piscivores is of considerable interest. The numerical data bearing on this question have been extracted from Table IX and pertinent information regarding weights added to form Table X. The four plankton- and bottom-feeding species (whitefish,

TABLE X. Percentage of piscivores compared with that of plankton and bottom feeding fish, numerically and by weight in the gill-net catch in the main lake and Hunter Bay, Lac la Ronge.

	Main lake % of catch		Hunter Bay % of catch	
	Numerically	By weight	Numerically	By weight
Four plankton and bottom feeders (Whitefish, ciscoes and two suckers)	92	75	88	64
Five piscivores (Trout, pike, walleye, burbot and perch)	8	25	12	36
Trout alone	2.9	11.5	5.9	26

ciscoes and two suckers) outnumber the piscivores, trout, pike, walleye and perch by 92% to 8% in the catch from the main lake and 88% to 12% in Hunter Bay. The comparable proportions by weight are 75 to 25 in the main lake and 64 to 36 in Hunter Bay. Thus in the catch from the main lake non-piscivores outweigh piscivores by 3 to 1 and in Hunter Bay by 1.8 to 1. Since all species of fish are not equally vulnerable to gill nets set along the bottom of a lake it should not be assumed that the proportions of various species in the catch as recorded above represent the true proportions of these species in the total population. Extensive use of gill nets set vertically in Lac la Ronge in 1959 indicated that the ciscoes are often much more available at levels far above the bottom. Thus the ciscoes probably represent a much larger fraction of the total population than would be suggested by the values in Table IX. An important difference between the two parts of the lake is that in the catch from Hunter Bay the lake trout make up two-thirds of the number of piscivores but in the main lake only one-quarter. This is consistent with our knowledge that Hunter Bay is essentially a deep, cold, oligotrophic lake ideally suited to lake trout whereas the main lake is more mesotrophic with much shallow water, better adapted to burbot, pike, and walleye. In the catch from the main lake the burbot outnumbers the lake trout and is no doubt its main competitor for food. In the Hunter Bay catch the lake trout greatly outnumbers the burbot so the latter is probably of minor significance as a competitor in this region.

The availability of lake trout to gill nets in Lac la Ronge may be compared to that in five other lakes in northern Saskatchewan which have been tested with similar standard gangs of net (Rawson, 1960). The numerical percentage of trout in the average catch from these lakes is as follows: Reindeer Lake 16.8; Wollaston, 11.2; Hunter Bay, 4.8³; Cree, 4.5; Athabaska, 2.4; La Ronge, 2.2³. A small amount of trout was caught in Amisk and Ile à la Crosse but no percentage recorded. It will be seen that Hunter Bay ranks third and the main part of Lac la Ronge sixth in the gill net catches of trout in these large lakes of northern Saskatchewan.

The average numbers of fish of all species caught in standard gang sets in 1958 and 1959 are greater than those caught in 1948 and 1949 both for the main lake and Hunter Bay, Table IX. The increase in the main lake and in Hunter Bay is about 16%. This increase is somewhat less than that which might be expected from the greater efficiency of nylon mesh nets.

The increase in catch of lake trout after 10 years was greater than that for most other species. In the main lake the average catch increased from 1.9 to 4.4 and in Hunter Bay from 4.6 to 7.9 trout per set. Specific data on the effectiveness of nylon and cotton nets in capturing lake trout in Lac la Ronge was obtained by Atton (1955a). He found that for nets of 1.5-, 2- and 5-inch stretched mesh the ratio of trout caught in cotton to nylon net was 1:1.26. The ratios of trout caught in 1948 to 1949 to those caught in 1958-59 are 1:2.3 in the main lake and 1:1.7 in Hunter Bay. Since the increase in catch after the 10-year period is more than twice as great as that which would be expected from the change to nylon nets, it seems safe to conclude that the availability of trout in Lac la Ronge has increased in the 10-year period. It will be noted later that the anglers' catch of trout has maintained a high level since 1952 and has increased in the years 1958 and 1959.

Changes in a fish population resulting from exploitation are commonly reflected in a decrease in the average length of fish taken in standard gear. The length distribution of trout taken in standard gangs from 1948 to 1959 is indicated in Fig. 7. A group of 325 trout caught from 1948 to 1953 had an average fork length of 23.08 inches and a prominent mode at 24 inches. In 1958, our sample of 304 trout averaged 23.15 and in 1959, 168 trout averaged 23.77 inches. Thus there is no evidence of change in the average length of trout in Lac la Ronge during this period.

An analysis of the age-length data was made to see whether any change in the year-class composition had taken place. Table XI compares the two groups. In both, the 8-year class is the most numerous and other year classes from 6 to 12 are represented by substantial numbers. Again no change is evident over the 10-year period.

³These percentages differ somewhat from those in the earlier paper (Rawson, 1960) because they include extensive data from 1958 and 1959. The sequence among the seven lakes remains the same.

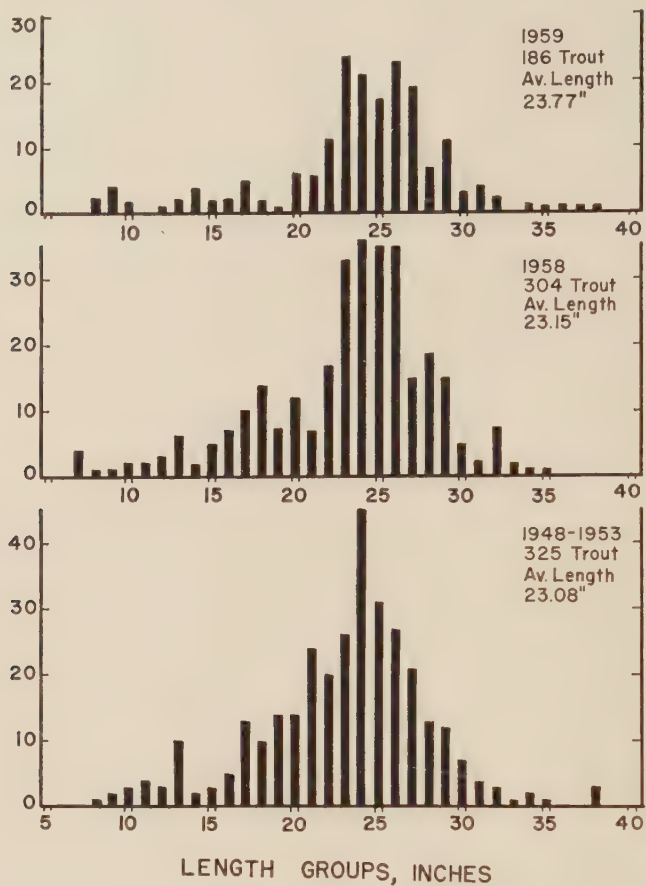


Fig. 7. Length frequencies of three samples of lake trout taken in standard gangs of gill net, Lac la Ronge, 1948 to 1959.

TABLE XI. Percentage composition by age-groups of trout taken in standard-gang nets in 1948-49 and in 1958.

	Number of trout	Age-groups								
		3-5	6	7	8	9	10	11	12	13-16
1948-49	118	7.4	8.5	15.4	22.8	17.6	11.4	7.4	4.0	5.5
1958	160	8.1	11.5	13.4	19.4	16.0	11.2	7.4	4.1	8.9

UTILIZATION OF THE TROUT POPULATION

The history of fishing in Lac la Ronge falls naturally into three periods. The first was a time of domestic fishing, when Indians, traders and travellers made use of the abundant fish population. Trading posts existed on the lake nearly 200 years ago and the sites of at least four are known. Records of the amounts of fish taken are very scanty but it is reasonable to assume that the fish taken

to feed the small number of residents and their dogs would have had little effect on the fish population.

The period of commercial fishing began about 1920 and the first records of production indicate a catch in 1922 of 229,500 lb, including 72,200 lb of trout. Taken by gill netting through the ice, these fish were frozen and hauled by horses 180 miles to rail-head at Prince Albert. After about 1930 most of the winter hauling was done by tractor. In 1945 a fish processing and freezing plant was built which allowed summer as well as winter fishing in 1946 and subsequent years. The commercial production of this period of nearly 30 years is shown in Table XII. The average annual trout production through this period was 113,505 lb.

TABLE XII. Commercial fish catch, in pounds dressed weight (head on) from Lac la Ronge in the years 1922-1950. From Rawson and Atton (1953).

Fiscal year ending March 31	Whitefish	Trout	Pickereel	Pike	Suckers	Others	Total
1922	69,300	72,200	20,900	27,700	21,700	17,700	229,500
1923	23,700	78,800	2,800	10,400	14,500	12,700	142,900
1924	53,200	91,300	6,800	8,100	10,700	7,200	177,300
1925	100,800	149,200	22,600	26,200	30,700	30,800	360,300
1926	214,200	188,000	23,000	23,600	37,200	37,000	523,000
1927	284,100	176,900	17,300	30,700	84,700	100,300	694,000
1928	336,900	184,900	22,900	20,100	27,800	25,800	618,400
1929	348,600	182,900	24,300	22,000	38,700	30,200	646,700
1930	251,900	164,600	14,300	18,100	26,500	22,500	497,900
1931	374,000	191,628	7,600	30,600	33,200	10,400	647,428
1932	78,400	36,800	1,500	1,100	7,900	6,200	131,900
1933	74,800	52,800	9,400	38,500	20,800	21,600	217,900
1934	55,526	77,520	8,836	16,530	10,330	5,400	174,142
1935	49,963	40,100	10,350	2,100	6,750	21,700	130,963
1936	47,323	34,343	1,850	3,470	9,300	16,200	112,486
1937	200,401	128,331	35,064	11,964	50,515	24,150	450,425
1938	157,956	261,654	17,858	9,393	25,800	33,750	506,411
1939	197,270	245,558	27,115	10,350	78,975	134,715	693,983
1940	72,059	133,300	21,676	16,896	78,176	78,610	400,717
1941	nil	nil	nil	nil	nil	nil	nil
1942	3,500	400	1,000	3,500	4,000	400	12,800
1943	17,400	2,070	4,346	3,720	1,560	1,100	30,196
1944	5,740	46,039	19,913	2,709	7,495	5,890	87,786
1945	5,046	120,832	42,048	13,043	10,750	10,070	201,789
1946	58,509	110,327	69,381	4,655	30,500	5,500	278,872
1947	48,115	151,581	77,403	6,355	4,867	25,000	313,321
1948	88,460	146,835	46,761	7,258	nil	nil	289,314
1949	34,488	59,130	53,129	2,886	9,311	nil	158,944
1950	26,812	50,089	30,916	2,346	1,330	nil	111,493
Totals	3,278,468	3,178,137	641,046	374,275	684,059	684,885	8,840,870
Average per year	117,088	113,505	22,895	13,367	24,430	24,460	315,745
Percentage	37.1	35.9	7.3	4.3	7.7	7.8	100.0

The third or angling period in the fishing of Lac la Ronge was made possible by the construction of a road from the Prince Albert National Park to La Ronge. This road was completed in 1947. In 1948 a small number of anglers visited the lake and many tourist cabins were built. In 1949 about 300 anglers fished the lake. Its reputation spread rapidly, roads and accommodation were improved and in 1950 the first great influx of 3,500 anglers occurred. The need for scientific information on the fish resource had been anticipated. In 1948 the writer began a detailed study of the lake and in 1950 an inclusive creel census was established.

The statistics from 29 years of commercial fishing were of considerable value in planning for the management of the angling fishery. They indicated a proven capacity for annual production of desirable fish of at least 1 lb per acre. The angling catch increased rapidly and there was no doubt that the fishery should be managed primarily for angling. It was clear, however, that the lake could also support an extensive commercial fishery for non-game species. The results of this continuing commercial fishery will be summarized before proceeding to a more detailed consideration of angling for trout.

Commercial fishing results for the 10 years from March, 1950, to March, 1960, are presented in Table XIII. The annual catch averaged about 250,000

TABLE XIII. Commercial fish catch, in pounds dressed weight (head on), from Lac la Ronge in the years 1951 to 1960 (fiscal year ending March 31).

Season	Whitefish	Trout	Pickarel	Pike	Suckers	Others	Total
Summer 1950	nil	nil	nil	nil	nil	nil	nil
Winter 1950-51	55,863	3,155	3,816	3,686	3,950	...	70,470
Summer 1951	67,264	86	657	924	42,490	500	111,921
Winter 1951-52	119,622	1,721	1,123	1,090	2,874	725	127,155
Summer 1952	nil	nil	nil	nil	nil	nil	nil
Winter 1952-53	149,034	6,860	993	374	3,285	...	160,546
Summer 1953	nil	nil	nil	nil	nil	nil	nil
Winter 1953-54	84,402	6,382	559	391	1,817	800	94,351
Summer 1954	nil	nil	nil	nil	nil	nil	nil
Winter 1954-55	204,673	19,109	2,417	2,574	11,123	41	239,937
Summer 1955	185,415	2,480	938	3,037	25,770	1,124	218,764
Winter 1955-56	108,359	7,810	3,443	641	64	111	120,428
Summer 1956	172,957	4,563	3,391	7,313	26,042	767	215,033
Winter 1956-57	29,948	4,983	1,394	392	...	24	36,741
Summer 1957	262,705	7,866	13,079	9,251	1,769	...	294,670
Winter 1957-58	58,970	5,438	1,847	436	128	...	66,819
Summer 1958	302,954	5,949	25,993	9,645	...	...	344,541
Winter 1958-59	nil	nil	nil	nil	nil	nil	nil
Summer 1959	311,975	3,907	24,077	4,621	...	...	344,580
Winter 1959-60	41,873	5,967	1,293	405	...	...	49,538
Average per year	215,601	8,628	8,502	4,478	11,931	409	249,549
Percentage	86.4	3.5	3.4	1.8	4.8	0.16	

lb as compared to 315,000 in the preceding 29 years. Vigorous efforts were made to increase the whitefish production while keeping the game fish catch to a minimum. The success of this program can be seen in the increase of whitefish from 37.1 to 86.4% of the catch, the decrease of trout from 35.9 to 3.5% and of the three game species combined from 47.4 to 8.7%. This result is especially commendable since the whole program was experimental, with administrators, fisheries biologists, conservation officers and commercial fishermen co-operating in attempts to find times, places and methods by which more whitefish and less game fish could be caught. The catches listed in Table XIII are separated as to summer (including autumn) and winter (which means through the ice, in December to March). In four summers no commercial fishing was carried on and none in the winter of 1958-59. Comparing summer and winter catches it will be seen that the summer operations were much more successful in avoiding game fish. This is attributed both to the greater segregation of species in summer and to the greater ease with which nets could be moved in this season. The catch in the 5 years in which both summer and winter netting was carried on is as follows:

In 5 summer catches averaging 230,000 lbs—trout 1.4%, all game species 6.4%

In 5 winter catches averaging 86,000 lbs —trout 9.7%, all game species 13.6%

Even higher proportions of whitefish and less game fish have been taken in some years by fishing during the spawning season of the whitefish, although heavy weather at this time of year made the operation difficult. With the information now available and with improved fishing boats it should be possible to extend the commercial fishery on Lac la Ronge while taking only negligible quantities of trout and other game fish. Recent observations suggest that, while the pike needs maximum protection, the walleye population may well support a modest commercial limit in addition to the present anglers' catch.

CREEL CENSUS

The creel census, begun in 1950, has been carried out each year by a full-time investigator. Since La Ronge is reached by a single highway and all the resort operators are located in one townsite, it has been possible to obtain from 65 to 90% coverage in the 11-year period under review. The creel census procedure was described by Rawson and Atton (1953).

Data concerning the catch of trout and its relation to the total anglers' catch from 1950 to 1960 are presented in Table XIV. The number of anglers fishing Lac la Ronge increased from 3,500 in 1950 to 7,000 in 1953, then decreased to 3,200 in 1957. This decrease was caused mainly by increasing numbers of anglers flying north to fish new lakes from camps on some 20 lakes, scattered over the northern third of the province. In 1958 to 1960 the number of anglers fishing Lac la Ronge has remained near the 11-year average. The catch per angler⁴

⁴Catch per angler, per visit which averaged about 4.5 hours fishing and frequently extended over two days.

TABLE XIV. Creel census records of anglers' catch in Lac la Ronge 1950 to 1960 with details of the lake trout taken.

	Number of anglers	Catch, all species	Catch per angler	Number of trout	Av. weight of trout	Total weight of trout	Trout in anglers' catch
	<i>no.</i>	<i>lb.</i>	<i>lb.</i>	<i>no.</i>	<i>lb.</i>	<i>lb.</i>	<i>%</i>
1950	3,500	204,000	58.3	8,882	7.35	65,280	32.0
1951	5,700	280,000	49.1	8,796	7.64	67,200	24.0
1952	6,250	251,000	40.1	5,642	6.68	47,690	19.0
1953	7,000	278,000	39.7	7,642	6.73	51,430	18.5
1954	4,700	205,000	43.6	5,272	6.61	34,850	17.0
1955	4,800	144,000	30.0	4,418	7.17	31,680	22.0
1956	3,900	150,000	39.0	4,032	7.44	30,000	20.0
1957	3,200	116,000	36.2	2,724	7.07	19,256	16.6
1958	4,150	150,000	36.1	4,933	8.21	40,500	27.0
1959	4,500	179,000	39.7	5,262	8.13	42,781	23.9
1960	3,800	200,000	52.6	6,427	6.97	44,800	22.4
Av.	4,682	196,091	42.2	5,821	7.27	43,224	22.0

began with 58.3 lb in 1950 and 49.1 in 1951. Reduced daily limits (discussed below) in 1951 and 1952 were involved in this initial decrease in the catch per angler. The catch fluctuated from 1953 to 1955 but remained remarkably stable at 36 to 39 lb from 1956 to 1959. In 1960 it rose sharply to 52.6 lb.

The anglers' catch of lake trout has varied with the number of anglers (fishing effort) but the percentage of trout in the anglers' catch has also varied. In the first two years, 1950 and 1951, the percentage of trout was high; then from 1952 to 1957 it varied from 16.6 to 22%. In the last three years, 1958 to 1960, the percentage has remained somewhat above the long-term average. The average weight per trout through the 11-year period was 7.27 lb, varying from 6.61 in 1954 to 8.21 in 1958. The continued large catch of trout, the stability of their average size and the continued catch of very large (trophy) trout mentioned above (Table IV), all seem to indicate that the trout population of Lac la Ronge is thriving and that present angling regulations are satisfactory for its conservation.

THE ANGLING FISHERY FOR TROUT

Lake trout are taken at Lac la Ronge with ordinary casting and spinning equipment from the break-up of ice until the surface waters of the open lake warm to about 12°C (54°F). This usually occurs about June 20 but may vary by as much as two weeks in different years. Surface fishing is again successful in mid- or late September when the surface water has again cooled to about 13°C (55°F) and trout have come into shallow water. During most of the season the trout are down in the cooler waters and until recent years were taken by conventional deep trolling equipment, metal lures on weighted metal, fibre or nylon lines. About 1957 some of the La Ronge fishing guides began to develop a new method

for catching trout locally termed "jigging". This technique was improved in 1958 and proved so efficient that in the summers of 1959 and 1960, at least 70% of the trout taken from deep water, were caught in this way. It is possible that this development is partly responsible for the increased anglers' trout catch in the years 1958-1960.

In the so-called "jigging" procedure the boat is anchored over a known "trout hole" usually at depths of 20 m (65 ft) or more. Bright metal lures are lowered with casting rod and line until they reach the bottom. They are then "snatched" away from the bottom reeling up quickly, often with a jerking movement. After reeling in about 10 m (30 ft) of line, if no strike occurs, the lure is lowered and the procedure repeated. Conventional deep trolling in the same areas will take considerably fewer trout although most of the very large trout are said to be caught by trolling.

Locations at which the trout are caught have been recorded by the creel census worker throughout the years of investigation. Since the catch in specific localities varies from week to week throughout the season and to a lesser extent from year to year, it is not possible to give the angler infallible instruction. However, the major generalization can be made that, after the early surface fishing fails, trout will be caught in all the areas indicated in Fig. 1 as deeper than 20 m (65 ft). In the early and late season surface fishing Nut Point and Hunter Narrows are favoured locations. In midsummer many trout are caught in the central islands area, e.g., west from Freeman Island to Stony Narrows, north to Bear Island and south and east of Meraste Point. The creel census indicates that the proportion of the total trout catch taken from Hunter Bay (including Hunter Narrows) has varied in different years from 33 to 69% and averages 45%.

Seasonal variation in angling effort and success is indicated in Fig. 8. The points plotted are the averages for bi-weekly periods through 11 summers, 1950 to 1960. Trout fishing in the last half of May is usually determined by the disappearance of the ice. Although the bay at La Ronge clears early and provides fine walleye fishing, the trout waters are often not accessible until the last few days of May. The trout catch is heaviest in June with the catch in the second half usually exceeding that in the first. The catch is still great in July but drops to a low in the second half of August, then rises slightly in September. In 1959 and 1960 September catches were 50% higher than the long-term average. The trout catch per angler throughout August and September is about the same as that in July, and greater than that in the first half of June (Fig. 8). Thus the anglers' preference for June fishing is not based on greater success in catching trout in this season.

The trout and other game fish caught by anglers in Lac la Ronge have always been well handled. The commercial processing plant froze much of the anglers' catch in whole or filleted form from 1950 to 1955. In recent years several of the outfitters operating the larger tourist camps and boat businesses have constructed their own filleting and freezing facilities. The angler from

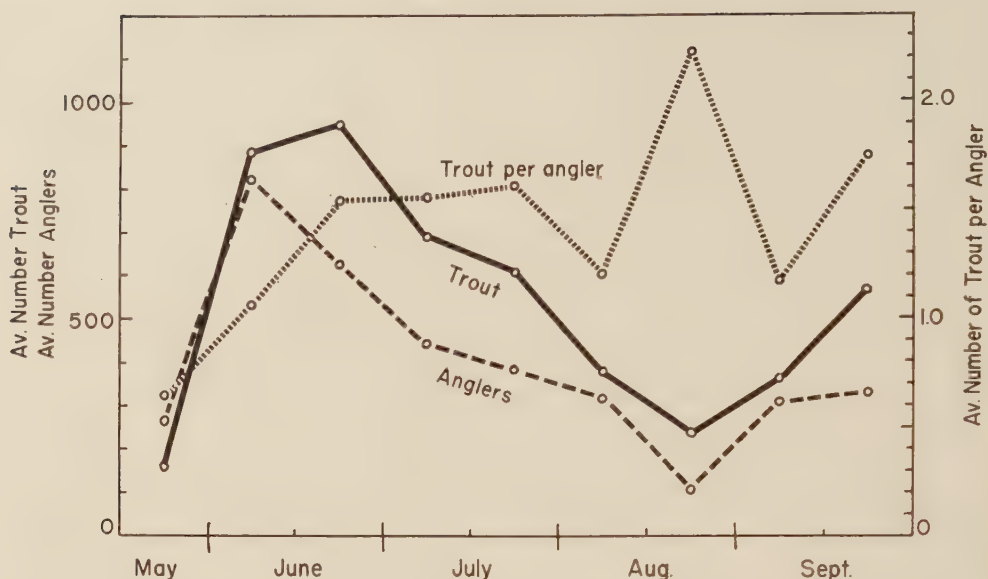


Fig. 8. Seasonal variation in the catch of lake trout, numbers of anglers and trout catch per angler in Lac la Ronge. The values plotted are averages for half-month periods throughout the years 1950 to 1960.

distant areas has thus been able to transport his catch in good condition and has been encouraged in good conservation practice.

The regulations in force when our creel census began in 1950 specified a daily limit per angler of 7 lake trout and a size limit of not less than 15 inches. In 1951 the daily limit was reduced to 5 fish. In 1952 the poundage of lake trout to be taken from Lac la Ronge was also restricted, the limit set being "not more than 4 lake trout not to exceed 25 pounds plus one lake trout". In 1958 the size limit was removed for trout and other species taken by angling. The 1951 and 1952 regulations apparently reduced the catch per angler to a level that could be maintained through the remainder of the 10-year period with minor fluctuations. Thus there was no need to consider further restriction. Such action might well have become necessary, had not the rapid development of "fly-in" fishing in more northern lakes reduced the total number of anglers on Lac la Ronge.

The annual harvest of trout from Lac la Ronge in the years 1950 to 1960 has averaged 43,000 lb taken by anglers (Table XIV) plus 8,000 lb taken in the course of the commercial whitefish operation. This amount, 51,000 lb per year, is only 45% of the average of 113,000 lb sustained by the lake over the period 1922 to 1950.

It may be questioned whether even a very large number of anglers could equal the efficiency of gill nets in catching trout from the lake. There is little doubt, however, that Lac la Ronge would well accommodate twice the number of trout anglers which fished the lake from 1950 to 1960.

ACKNOWLEDGMENTS

The writer is indebted to the Fisheries Branch, Saskatchewan Department of Natural Resources, for the opportunity to carry out this investigation and for complete financial and administrative support. The field data were obtained through vigorous and conscientious efforts of numerous student field assistants. Conservation Officers at La Ronge helped in many ways. Special acknowledgment is due to Mr D. Snell who directed the spawn-taking operations and to Mr F. M. Atton, Provincial Fisheries Biologist, who contributed valuable suggestions for the field program and in the analysis of data.

SUMMARY

1. Lac la Ronge, a lake of 500 square miles (1425 km²) lying across the margin of the Precambrian, provides an unusually favorable environment for the production of the lake trout, *Salvelinus namaycush*.

2. Lake trout spawn on shallow rocky reefs in Lac la Ronge during the first week in October when water temperatures are about 10 to 11°C (50–51.8°F). Sexual maturity is usually reached in 6 or 7 years. The bulk of the spawning trout are between 21 and 28 inches fork length. A few mature trout, possibly 10%, fail to spawn in any single year.

3. Growth, as revealed by a sample of 900 trout from Lac la Ronge, is slower than that in small lakes of Ontario and New York State, similar to that in the Great Lakes and Great Slave Lake and faster than that in Great Bear Lake. No difference was found in growth of male and female fish and no change in growth rate in two large samples taken ten years apart. There was, however, a distinct difference in growth rates between trout in the main lake and those in the deeper and more oligotrophic Hunter Bay. Trout in the main lake made faster early growth, then slowed and were overtaken at about 12 years by those from Hunter Bay. A comparable difference was demonstrated by Kennedy (1954) between east and west parts of Great Slave Lake. Length-weight studies show that the trout of Lac la Ronge are well nourished, the larger specimens being considerably heavier than those of equal length and age from Great Slave Lake. Lac la Ronge trout grow to a large size; at least 33 fish between 30 and 41 pounds were caught in the years 1949 to 1960.

4. The main foods of the lake trout in Lac la Ronge are ciscoes, whitefish and ninespine sticklebacks. These with 8 other species of fish made up more than 90% of the food of adult trout. The crustaceans *Mysis relicta* and *Pontoporeia affinis* were important invertebrate foods, especially for the younger trout. The latter ate considerable numbers of sculpins and ninespine sticklebacks.

5. The chief parasites of the lake trout were tape-worms, two in the alimentary canal and a third, *Triaenophorus crassus*, encysted in the flesh. Nematodes and parasitic copepods were also collected.

6. Depth distribution and seasonal movements of lake trout were related primarily to temperature. Extensive gill-netting through several summers showed that trout were widespread from the break-up of ice in late May until the upper water warmed to about 14°C (57.2°F), usually near the end of June. The trout were then concentrated in the water deeper than 20 m (65 ft) and at temperatures mostly less than 10°C (50°F) for the remainder of the summer. They came into shallow water again after the autumn turnover and cooling to about 13°C (55.4°F) in mid- or late September.

7. Tagging of 429 trout and recovery of 60 indicated extensive movements. Twenty-one of those recovered were caught from 4 to 22 miles (6-35 km) from the point of tagging. One-twelfth of those recaptured had moved from the main lake to Hunter Bay or vice versa.

8. The catches from 169 gill net sets suggest the relation of trout numbers and weight to those of other species of fish in Lac la Ronge. In the main lake trout make up 11.5% of the weight of the catch, other piscivores 13.5% and plankton and bottom feeders 75%. Trout make up 26% of the catch in Hunter Bay. The average catch of trout in gill nets in 1958 and 1959 was greater than that in 1948 and 1949 even after making allowance for the change from cotton to nylon nets. The average size of trout caught in nets and their age composition remained unchanged after the 10-year period.

9. Commercial fishing in the 29-year period ending in 1950 took an average of 113,500 lb of trout and a catch of all species of 315,700 lb per year. Commercial fishing has continued in the years 1951 to 1960 with an average catch of 250,000 lb per year but the lake trout taken in this operation have been held to an average of 8,600 lb per year or 3.5% of the catch. In this way the trout has been protected for angling without losing the valuable commercial fishery for whitefish.

10. A continuous creel census shows the average trout catch from 1950 to 1960 to be 5,800 fish weighing 43,000 lb. The catch per angler decreased in 1951 and 1952 because of legal restriction but stabilized at about 36 lb. The number of anglers and the catch of trout has risen in the years 1958, 1959 and 1960. The average weight of trout caught has increased slightly and the number of very large "trophy" trout has been maintained.

11. Since the Lac la Ronge lake trout population appears to be thriving in 1960, and since the present annual catch is about 51,000 lb as compared to 113,000 lb per year taken over an earlier 30-year period, it is suggested that the lake could support an angling catch of trout at least double that which is now taken.

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A Limnological Reconnaissance of a Nova Scotian Brown-water Lake¹

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ABSTRACT

Summer hydrography and biota of a Nova Scotian brown-water lake are described. A bloom of a dinoflagellate was noted. Zooplankton was plentiful. With a range in pH of 4.3–4.8, mollusks were absent. *Chaoborus* dominated in the poor bottom fauna. Standing crop of fish was low at 19 kg per ha. Yellow perch were most numerous, exhibiting a decline in growth rate to age III, then increasing when the fish reached a size to be piscivorous. Fish-cultural implications are briefly discussed.

INTRODUCTION

THE PRINCIPAL LAKE DISTRICTS of the Canadian Atlantic provinces of New Brunswick and Nova Scotia lie in igneous rock formations. Waters in these areas are characteristically soft. Frequently they are stained in varying degree by humic extractives, derived from marginal bogs or from drainage of bogs, swamps and soils of the forest floor in the watersheds. Boar's Back Lake, Digby County, Nova Scotia, is among those lakes in which high acidity and colour of water are most extreme for the region.

Boar's Back Lake was treated with copper sulphate in 1936 to destroy fish competitors and predators of brook trout (*Salvelinus fontinalis*) (Rodd, 1937). The writer was associated with personnel of the then Fish Culture Branch of the Department of Fisheries, Ottawa, in this operation, and made sporadic limnological observations during the years 1936–38. Data most pertinent to the copper sulphate treatment have been published (Smith, 1938a, 1940). Since that time chemical characteristics of waters in a number of lakes in New Brunswick and Nova Scotia, including Boar's Back, have been reported (Gorham, 1957; Hayes and Anthony, 1958; Smith, 1952). The following account is presented to associate certain qualitative and quantitative aspects of the biota of Boar's Back Lake with the physical and chemical nature of its waters. Some notion is thereby gained of the feasibility of improving the sport fisheries in acid, brown-water lakes of the area by management techniques such as stocking, destruction of undesirable fish species, and others.

LOCATION AND MORPHOMETRY

Boar's Back is a headwater lake tributary to the Carleton Branch of the Tusket River, southwestern Nova Scotia (65°57'W, 44°09'N) (Fig. 1). A survey bench mark at the lake shows an altitude of 223 feet (68 m) above mean sea level.

The lake receives drainage from a forested area of Precambrian quartzites. Its waters are deeply stained, but it is not a bog lake in the sense that it is peripherally surrounded by a true bog. Rather, much of the shore-line is rocky.

¹Received for publication December 5, 1960.

Boar's Back Lake has an area of 55.8 acres (22.6 ha). The maximum depth is 26 feet (8 m), and the mean depth, 8.5 feet (2.6 m). An estimate of volume is $20,655 \times 10^3$ cubic feet (585×10^3 cu m). The shore and volume developments are 1.49 and 1.11 respectively.

HYDROGRAPHY

Chemical characteristics of the surface water of Boar's Back Lake given by Hayes and Anthony (1958) are as follows: pH, 4.7; M.O. alkalinity as ppm CaCO_3 , 5.7; ppm of Ca, 1.3, of Mg, 1.0, and of Na+K, 4.0; colour as ppm Pt, 163; conductivity in megamhos at 20°C , 41. Conductivity appears high for such acid waters. Hayes and Anthony (1958) found that conductivity did not continue to decline with increasing acidity in acid-water Nova Scotian Lakes, but actually rose when pH values fell below 6. They attribute this seeming anomaly in part to contributions of salt from sea winds. Influence of salt carried by sea breezes and gales in the electrolyte content of coastal fresh waters has been noted widely, not only for Nova Scotia (Gorham, 1957) but elsewhere as well, by Yoshimura (1936) and others.

The writer found that the waters of Boar's Back Lake were thermally stratified in summer (Fig. 2). Bottom water temperature at 8 metres on August

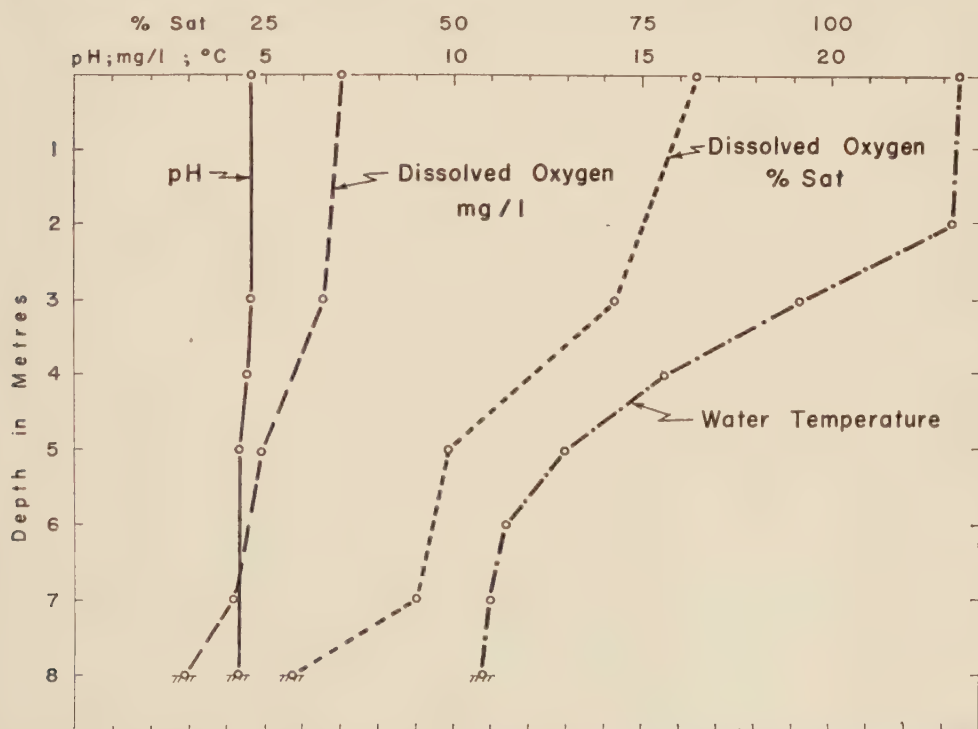


FIG. 2. Temperature, dissolved oxygen and pH values of water in Boar's Back Lake, August 10, 1938.

10, 1936, was 15.4°C. On the same date in 1938 it was 10.8°C. Between these two years at least, there was apparently considerable difference in the temperature level to which the spring period of homothermy persisted, with advance of the open-water season. A higher dissolved oxygen value for bottom water in 1936 than in 1938 (3.8 as against 2.9 mg per litre) also suggests that the homothermous condition persisted to a later date in 1936.

With summer stratification, pH and dissolved oxygen values were reduced in the hypolimnion (Fig. 2). The lowest recorded oxygen content at the bottom was 2.9 mg per litre on August 10, 1938. However, the volume of water with low oxygen values was a small part of the total lake volume. Reduction of dissolved oxygen was not seriously adverse to life in much the greater part of the volume of Boar's Back Lake.

Acid brown-water (dystrophic) lakes may have a good bacterial flora. Hayes and Anthony (1959) found a positive correlation between bacterial counts and colour for Nova Scotian lakes. Diminution of dissolved oxygen in brown-water lakes may be attributed in large part to bacterial decomposition of the allochthonous organic matter which imparts the brown colours. Hutchinson (1957) has pointed out that purely chemical processes, and possibly photo-oxidation, may also be involved. Whatever the processes, there appears general agreement that allochthonous rather than autochthonous organic materials are dominantly concerned. Accordingly, a reduced oxygen content in brown-water lakes, such as Boar's Back, is not considered as an index of eutrophy.

PHYTOPLANKTON

Qualitative phytoplankton samples were collected during July 1936 with a number 20 silk plankton net. Specific identifications of constituents have been reported by Hughes (1949) with the locale designation "N.S. Digby lake". The number of species of algae in the samples was small, as may be seen in the Appendix of this paper.

The dinoflagellate, *Peridinium limbatum*, was dominant in the samples. The species has been reported as rather rare in bogs and soft-water lakes of Wisconsin and Minnesota (Prescott, 1951), and a Charlotte County lake, New Brunswick (Hughes, 1949). Its occurrence in Boar's Back Lake was noteworthy in that it was sufficiently abundant to form a moderate water-bloom during July 1936. The most visible manifestation of the bloom was a "film" at the surface of the lake when calm in early morning. The phytoplankton of acid brown-water lakes is almost invariably reported to be quantitatively poor, rarely with development of water-blooms (Thienemann, 1925). The blooming of *P. limbatum* under the dystrophic conditions in Boar's Back Lake would thus appear to have been an unusual observation.

Desmid species are prominent qualitatively in the phytoplankton (Caledonian type of algal flora) of lakes of New Brunswick and Nova Scotia that receive drainage from areas of igneous rocks (Smith, 1938b, 1952; Hughes, 1949). However, the number (5) of desmid species found in Boar's Back Lake was decidedly

less than the 51 species recorded for Lake Jesse, and the 25 for Tedford Lake, which are two soft-water lakes also located in southwestern Nova Scotia (Smith, 1938b; Hughes, 1949). The acidity of Boar's Back Lake (pH 4.3–4.7) is definitely higher than encountered in Jesse (pH 6.3–6.6) or in Tedford (pH 5.6–6.4), as is also the colour. The situation in Boar's Back Lake may reflect inadequate sampling temporally. However, Ruttner (1953) noted a decline in number of desmid species in bog habitats of the Lunzer Obersee environs in Austria as the pH values declined from 4–5.5 to 4.0 and below. Accordingly, there are grounds to suspect that the rather extreme dystrophic environment in Boar's Back Lake conditioned an algal flora aberrant, qualitatively and quantitatively, from that which has usually been encountered in less acid, yet soft-water lakes common in the Maritime region.

ZOOPLANKTON

The zooplankton was sampled quantitatively with a Juday 10-litre plankton trap equipped with a number 18 plankton net. Samples were obtained at 4 stations on July 20, 1936. Five hauls with the trap were made at 1-metre depth intervals. The depths of water at the 4 stations, numbered 1 to 4 in Table I, were 1.5, 8, 2 and 4 m. The zooplankters in five 1-millilitre sub-samples, each taken directly from the 50-litre samples, were enumerated and numbers per litre calculated from these counts (Table I). Additional qualitative zooplankton

TABLE I. Zooplankton in Boar's Back Lake, as number of individuals per litre. Asterisks indicate presence but less than one per litre. Blank spaces indicate absence from counts.

Station	Depth	<i>Daphnia</i>	<i>Diaphanosoma</i>	<i>Holopedium</i>	<i>Bosmina</i>	<i>Immature copepods</i>	<i>Diaptomus</i>	<i>Mesocyclops</i>	<i>Polyarthra</i>	<i>Kellicottia</i>	<i>Keratella</i>	<i>Trichocera</i>	<i>Chaoborus</i>
1	0–1	...	37	1	9	12	36	5	37	...	25	8	...
2	0–1	...	38	1	5	42	36	2	6	...	11	1	*
	1–2	...	11	*	4	19	10	1	3	...	3	*	*
	2–3	...	8	*	6	12	5	*	3	*	2	1	*
	3–4	*	9	1	7	3	3	1	1	3	1	...	*
	4–5	1	3	*	2	2	2	3	*	6	1	...	...
	5–6	*	3	...	*	3	1	4	1	10	1	...	1
	6–7	1	3	...	1	7	2	1	1	5	1	...	*
	7–	1	2	...	1	7	1	*	1	4	*	...	*
3	0–1	...	40	2	4	9	29	5	19	...	19	7	*
	1–	...	23	*	5	12	17	4	9	...	14	2	*
4	0–1	...	37	*	11	18	42	2	12	...	9	1	*
	1–2	...	11	1	6	14	16	2	5	...	3	1	...
	2–3	...	7	*	7	7	6	1	3	2	1	1	...
	3–	...	4	2	5	2	3	2	1	3	1	*	...

samples were collected in 1936, and later in 1937 and 1938, with a number 5 plankton net.

A list of zooplankters found in the several samples is given in the Appendix. For the most part the species encountered are common in soft waters of New Brunswick and Nova Scotia (Smith, 1938a, 1952), as well as being more cosmopolitan in distribution. Rotifers were prominent, and this has been generally noted for bog waters (Harnisch, 1929; Gorham, 1931). Cladocerans and copepods, however, appeared to play a more prominent role in the zooplankton of Boar's Back Lake than was observed by Gorham (1931) for both acid and alkaline bog lakes in northern Michigan.

The two diaptomids found in Boar's Back Lake are sharply contrasted in their distribution in the Maritime Provinces. Whereas *Diaptomus minutus* is almost omnipresent in limnetic plankton, *D. pygmaeus* has not been noted elsewhere in the considerable number of Maritime lakes that have received attention. Pennak (1957) has noted that the simultaneous occurrence of two or more species of crustacean zooplankters of the same genus in limnetic communities of small lakes is unusual.

The recorded distribution of *D. pygmaeus* is in ponds and lakes of northeastern United States (Wilson, 1959). Its occurrence in Nova Scotia is thus within the expected geographic range of the species. Although the restricted geographic range and sporadic occurrence of many diaptomids is well known, the seeming isolation of *D. pygmaeus* among Canadian Maritime waters to Boar's Back Lake, with its more extreme dystrophic conditions, suggests a stenokous species, strongly alkaliphobic. Unfortunately, neither Pearse (1906), who first described the species, nor more recent recorders provide chemical data which would permit further evaluation of this view. The seeming isolation of *D. leptopus* var. *piscinae* Forbes in the most acid of the Michigan bog lakes studied by Gorham (1931) is possibly a parallel situation.

Zooplankters were numerous in Boar's Back Lake (Table I). For most species, however, their numbers declined quite sharply with depth. At station 2 the number per litre of surface water approximated 140, while near the bottom at 8 m the number was about 18. *Daphnia* and *Kellicottia* were exceptions in that they were not encountered until a depth of 3-4 m had been reached. Larvae of *Chaoborus* were taken in fair numbers in the plankton samples. *Chaoborus* reacts negatively to light, retreating to deep waters or the bottom in clear-water lakes during the day, then nocturnally migrating toward the surface. Its planktonic occurrence at practically all depths in Boar's Back Lake in daytime was associated with poor light penetration occasioned by the high colour of the water.

The water of Boar's Back Lake to a depth of about one metre contained about 140 macrozooplankters per litre. These represented a dry weight of approximately 300 mg/cu m. We are here concerned with one estimate of standing crop, which is restricted to surface waters. The value of the data for comparisons is definitely limited. Nonetheless, the data indicate, so far as the zooplankton

is involved, at least a mesotrophic level of production (Birge and Juday, 1922). Thienemann (1925) in his systematic characterization of European lakes recorded the zooplankton of dystrophic waters as often being rich.

BOTTOM FAUNA

The bottom fauna was sampled with an Ekman dredge (81 sq in; 522 sq cm) at 30 stations, July 11-17, 1936 (Fig. 1). As much of the bottom materials as possible was washed through a set of three screens of which the finest had a mesh gauge of 1 mm. The organisms, while still alive, were sorted from the remaining debris.

Numbers of bottom organisms taken at various depths are given in Table II.

TABLE II. Number of organisms in the bottom fauna of Boar's Back Lake, July 11-17, 1936. Samples were taken of 522 sq cm area each; figures shown are the total numbers taken in all samples at the depths indicated.

Depth of water (m)	0-2	2-3	3-4	4-5	5-6	6-7
Number of samples	8	10	5	3	2	2
<i>Chaoborus</i> larvae	22	122	84	54	33	30
<i>Chaoborus</i> pupae	3	15	24	11	3	3
Chironomid larvae	6	8	5	6	6	11
Caddisfly nymphs	2	10	1	3	1	0
Mayfly nymphs	0	1	0	1	0	0
Damselfly nymphs	0	0	1	0	0	0
Beetle larvae	2	1	0	0	0	0
<i>Asellus</i> sp.	1	0	0	1	0	0
<i>Hyaella azteca</i>	0	2	0	0	0	0
Oligochaeta	3	1	0	1	0	0
Totals	39	160	115	77	43	44
Av. no. per sample	4.4	16.0	23.0	25.7	21.5	22.0
Range	1-28	9-32	15-38	7-43	21-22	21-23
No. per sq m	84	307	441	492	412	422

The summer standing crop of bottom macroorganisms was poor, both qualitatively and quantitatively. To be anticipated from the high acidity and low carbonate content of the water, no mollusks were found in the dredge samples, or by search of the littoral areas. The bottom fauna consisted almost entirely of immature insects. Of these, *Chaoborus* larvae and pupae (84% by number) were dominant. As already noted, *Chaoborus* may be considered both as a bottom organism and as a plankter. In Boar's Back Lake it was found distributed throughout the volume of lake during the day which was the time when the bottom samples were collected. Thus, neither the plankton nor bottom samples alone gave a good picture of total numbers of *Chaoborus* in the lake. Based on our samples, and considering that they showed a reasonably representative distribution of *Chaoborus* in Boar's Back Lake on a July day, estimates of numbers in the lake

disclosed that the ratio of these midges as plankton to those as bottom organisms was 2.2:1 (140×10^6 plankton as against 63×10^6 bottom organisms). If *Chaoborus* larvae and pupae were excluded from the bottom fauna, as they would be to a large extent had the bottom samples been taken at night, the summer standing crop of bottom organisms would indeed be small.

Particularly where immature insects dominate, and because of their emergence as adults, summer standing crops of bottom organisms are often minimal for the year. Notwithstanding this probability, our sampling indicates that the bottom fauna of Boar's Back Lake was poor at any season, in agreement with the findings of other investigators of brownwater lakes. The total dry weight of the bottom organisms taken in the 30 samples in July was 0.188 g, or 0.120 g/m².

FISH

STANDING CROP

Boar's Back Lake was treated with copper sulphate (3.03 ppm $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$) on August 5, 1938 (Smith, 1940). Counts of killed fish were made on six shore-line areas, each 85 m (279 ft) in length, selected before the poisoning (Fig. 1). These areas covered about 18% of the lake's perimeter. The fish were enumerated and removed daily for 12 days following the poisoning, that is until very few individuals were found. All fish on certain smaller shore areas, included in the above, were collected and preserved for subsequent length, weight and age determinations.

Seven species of fish were found in the lake, of which yellow perch (*Perca flavescens*) were most plentiful (Appendix). Estimates of the numbers and weight of fish in the standing crop are given in Table III. One may safely assume that the horizontal and vertical distribution in the lake at the time of poisoning differed among the several species. This situation probably affected the relative numbers of the various species found on the sampling areas. Westerly winds prevailed during most of the investigational period. Accordingly, in making population estimates, the perimeter of the lake was arbitrarily divided into three equal sections, eastern, central and western, for each of which two collection areas were considered representative.

It was assumed in making the estimates of standing crop that (1) all fish were killed by the copper sulphate, and (2) they came ashore after being poisoned. There are no data to gauge how well these assumptions were met at Boar's Back Lake. Quite commonly a few fish survive treatment of lakes with copper sulphate or rotenone. Neighbouring Tedford Lake was treated with copper sulphate in 1936. Later in 1953 rotenone was added to this lake under the auspices of the Fish Culture Development Branch of the Canada Department of Fisheries. Killifish, golden shiner, bullhead, and eel were found to have repopulated the lake either from survivors of the first poisoning or from immigrants. However, yellow perch and white perch (*Morone americana*), which had been dominant in the fish population of Tedford Lake in 1936, were absent in 1953. With

TABLE III. Estimates of number and weight of fish in standing crop, Boar's Back Lake, August 1936.

	Brook trout	White sucker	Golden shiner	Brown bullhead	American eel	Banded killifish	Yellow perch
I—Numbers							
Collection area 1	...	19	52	48	19	89	1,057
2	...	10	27	74	10	35	632
3	...	5	44	54	5	21	349
4	...	11	5	81	11	35	289
5	...	7	17	44	7	16	531
6	...	7	38	79	7	29	1,231
Estimated							
Eastern third of lake	...	143	495	699	143	649	12,584
Central third of lake	...	132	242	649	94	281	6,397
Western third of lake	...	88	270	743	88	308	3,509
Total for lake	23	363	1,007	2,091	325	1,238	22,490
II—Weight							
Number in sample for weight	20	19	54	45	12	91	822
Weight of sample	2.84	10.66	0.51	2.29	0.23	0.31	3.63
Calculated for lake kg	3.3	203.7	9.5	106.4	6.2	4.2	99.3
" " " lb	7.3	449.2	20.9	234.6	13.7	9.3	219.0
III—Totals for lake							
Number of fish	27,537		Number per ha		1,218		
			per acre		493		
Weight of fish, kg	432.6		kg per ha		19.1		
lb	954.0		lb per acre		17.1		

respect to the second assumption, Krumholz (1948) and Ball (1948) were able to recover 84 and 54% respectively of marked fish introduced into small Michigan lakes before poisoning with rotenone. In part, poor recovery was attributed to entanglement of fish in bottom vegetation, and to failure of individuals to float after sinking to the bottom in cool, oxygen-depleted deep water. Such collection conditions were definitely less adverse at Boar's Back Lake, but the estimate of 17 lb per acre (19 kg per ha) for the standing crop of fish should be considered minimal. However, an upward revision, even to doubling the estimated standing crop, would still indicate a small fish biomass (Carlander, 1950).

COMMENTS ON CERTAIN SPECIES

BROOK TROUT. The entire shoreline of Boar's Back Lake was searched for this species on three occasions after the poisoning. Only 23 specimens were found. Nine individuals in a preserved sample of 20 trout appeared to be age II, with a mean fork length and standard deviation of 17.6 ± 1.5 cm, weight of 66 ± 11.5 g, and condition index (K) of 1.19 ± 0.080 . For the other 11 specimens in the sample, ranging in length from 21.3 to 30.7 cm and in weight from 126 to 361 g, it was not possible to read their scales with acceptable confidence.

Spawning facilities for trout at Boar's Back Lake, either in tributaries, in the outlet for considerable distance below the lake, or in the lake itself, are very limited, if any exist at all. In view of this, and the absence of young trout, it would appear that the small population consisted of upstream migrants into the

lake. It is not to be inferred, however, that Boar's Back Lake would be appreciably more productive of trout if stock were introduced. Advanced brook trout fry were introduced in the lake after the poisoning, 42,000 in 1938 and 50,000 in 1945 (Rodd, 1940, 1947). In 1956, 4000 fish of the year were planted. Although no creel censuses were subsequently maintained, guides and anglers reported few or no trout taken from Boar's Back Lake after the plantings (Fishery Officers B. H. Comeau, J. H. Thibault, personal communications).

WHITE SUCKER. Numerically suckers held a subordinate position in the fish population. They were relatively large individuals, however, with the result that this species made up a good proportion (47%) of the fish biomass in 1936 (Table III). The fork length range encountered in a sample of 19 fish was 14.3 to 44.0 cm. Ages were not determined, but as might be judged from length frequencies, two year-classes dominated, one (9 specimens) with a mean fork length of 36.4 cm and weight of 578 g, the other (6 specimens) at 41.5 cm and 774 g. The condition index (K) of the larger suckers (33.5 to 44.0 cm) was low, at 1.15 ± 0.182 . Carlander (1950) gives a range of 1.70 to 2.26 in average values for this species in several American lakes. There was a very low quantity of bottom fauna to support a bottom-feeder such as the sucker.

Sucker populations in Maritime headwater lakes are often maintained from spawning in outlets. The absence of young suckers indicates that this was not the situation at Boar's Back Lake, for certain years just prior to 1936 at least. Quite possibly suckers in Boar's Back Lake were consistently unsuccessful in maintaining a population in the lake, and, as postulated for brook trout, the population present in 1936 was recruited from larger lakes lower in the river system. Recruitment would seem most probable from spawning fish, some of which continued to move upstream instead of dropping back into the lake of their origin, in this case larger Hunter Lake to which the outlet of Boar's Back Lake is tributary. The possibility is considered since, if true, the low estimated standing crop of 19 kg of fish per hectare, initially viewed as having been produced in Boar's Back Lake, would be materially lower, reduced by a possible maximum of 9 kg/ha if no sucker growth occurred in the lake.

AMERICAN EEL. This species is successful in Maritime lakes generally but, aside from brook trout, it was the least numerous of the fish in Boar's Back Lake (Table III). The relatively small number may in part reflect the unproductive character of the lake. However, Smith and Saunders (1955) noted that smaller standing crops of eels were associated with greater distances of lakes from sea. Lake populations of the catadromous eel are largely recruited at the elver stage from the sea. Boar's Back is a headwater lake with numerous lakes in the river system below, which could hold upward-moving young eels. This situation is advanced as an important factor in the low population of eels in Boar's Back Lake.

YELLOW PERCH. This species made up 82% of the estimated 1936 fish population numerically, but contributed only 23% of the total fish biomass (Table

III). Size for age was small, appreciably smaller than in neighbouring soft-water Lake Jesse (Smith, 1939) and much below that in more eutrophic waters (Carlander, 1950).

The growth pattern for yellow perch in Boar's Back Lake differed from that most often noted for fish populations (Ricker, 1958). However, this pattern can emerge for species, such as perch, which feed on their own young, and are capable thereby of self-regulation of population (Nikolsky, 1956). These are species that by this characteristic in feeding can very well maintain populations when other foods for mature fish are scarce. Data for the perch from Boar's Back Lake appear illustrative of the bionomics of this type of fish population.

The growth rate declined from age 0 to age III, then increased quite sharply, to fall off again amongst the oldest fish (Table IV, Fig. 3). This growth pattern

TABLE IV. Age, length in centimetres, and weight in grams, with standard deviations, of perch from Boar's Back Lake. Age 0 perch were not weighed individually.

Number in sample	Age	Fork length	Weight
126	0	3.7 ± 0.36	0.7
438	I	6.1 ± 0.47	2.4 ± 0.62
107	II	7.3 ± 0.41	4.6 ± 0.93
78	III	8.1 ± 0.41	6.2 ± 1.56
50	IV	9.2 ± 0.76	9.8 ± 2.67
7	V	11.9 ± 0.98	22.8 ± 6.86
3	VI	15.8	56.6
3	VII	19.2	102.8

would seem quite consistent, however, with ecological conditions, particularly with respect to food supply, encountered by the perch, and with the feeding habits of the species. Zooplankters, bottom organisms, and fish serve as food of yellow perch (Pearse and Achtenberg, 1921; Parsons, 1950). In most habitats more productive than Boar's Back Lake, bottom organisms are an important sustaining food source for all except possibly the youngest fish. In general, size of preferred food organisms increases with size of fish. In Boar's Back Lake the supply of zooplankters was quite good, but in contrast bottom organisms were scarce. There would appear to have been a deleterious effect on both growth and survival with increasing age, largely as a result of few bottom organisms. However, the relatively small number of perch that became big enough to be piscivorous found a good source of food in small fish, particularly their own young. The fish food supply was small but so was the number of feeders. Growth rate of the older perch could then increase consistent with, but not reflecting the low level of production in the lake, especially that of bottom organisms. The growth pattern of the perch in Boar's Back Lake provides an example where size rather than age determined growth rates, in this instance

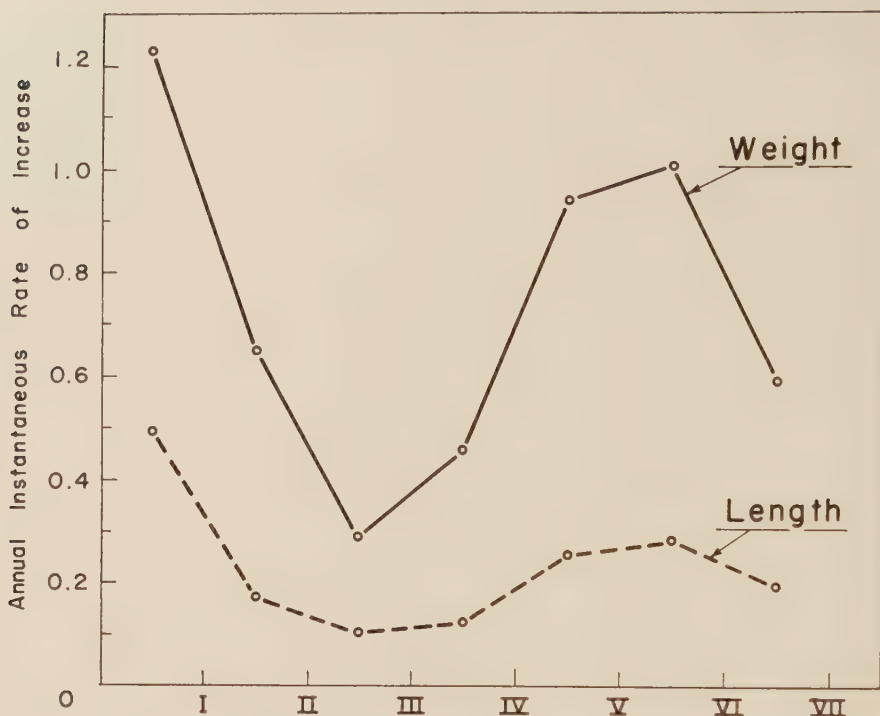


FIG. 3. Annual instantaneous rate of increase in length and weight of yellow perch from Boar's Back Lake.

where there was the "ecological opportunity" when adequate size to feed on fish was attained (Parker and Larkin, 1959).

A growth pattern similar to that for perch in Boar's Back Lake was also evident, but in a much less striking manner, for *Perca flavescens* in Wisconsin lakes (Schneberger, 1935) and for some year classes of *P. fluviatilis* in Windermere (Le Cren, 1958). Bottom organisms can be an important and adequately sustaining source of food for perch populations (Pearse and Achtenberg, 1921; Parsons, 1950). Thus where the bottom fauna is rich, there may be no depression in growth rate of intermediate sizes of perch such as was found in Boar's Back Lake.

DISCUSSION AND SUMMARY

Dystrophy is manifest in varying degrees in a majority of lakes in the eastern Maritime provinces of Canada. Boar's Back is among those lakes of the region exhibiting dystrophic conditions most extremely. Associated with this was a very poor production of bottom fauna and of fish, as might be gauged from the standing crops. However, production appeared better at other trophic levels. A bloom of a dinoflagellate was noted, and zooplankters were numerous, especially

in the epilimnial waters. Although the bloom of the dinoflagellate, *Peridinium limbatum*, at least superficially suggested eutrophy, Margalef (1958) has pointed out these algae actually "immobilize organic matter and slow down the turn-over" since they are poorly grazed.

The stocking of dystrophic Boar's Back Lake with the indigenous brook trout did little to improve angling, even when other species were eliminated. Johnson and Hasler (1954) obtained more favourable results from stocking non-indigenous rainbow trout in small dystrophic lakes of Wisconsin. This was done in the knowledge that rainbow trout may feed at all ages on zooplankters which usually predominate in the fauna of dystrophic waters. Rainbow reputedly tolerate higher water temperature than will brook trout. The non-indigenous smallmouth black bass grows well and appears to utilize the productive capacity of dystrophic lakes in southwestern New Brunswick to better advantage than the native brook trout (Smith, 1942).

Stocking non-indigenous species may result in better utilization of the productive capacities of dystrophic lakes by desired sport fish, yet it does not raise the basically low level of production in these waters. Attempts have been made in this latter direction by liming in Wisconsin and Michigan dystrophic lakes (Stross and Hasler, 1960; Waters and Ball, 1957) and in Scottish soft-water lakes (Holden 1959). Favourable but inconsistent results were observed in production at the lower trophic levels, but improved fish production was minor, if at all. On the whole, dystrophic waters still remain a challenge in management for feasible, worthwhile improvement in production.

ACKNOWLEDGMENT

Laboratory assistance from Miss Mary Holmes is gratefully acknowledged. Illustrations were made by Mr P. W. G. McMullon.

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APPENDIX

List of organisms identified from Boar's Back Lake.

ALGAE (identified by E. O. Hughes)

Anabaena sp.
Peridinium limbatum (Stokes) Lemm.
Characiopsis cylindricum (Lambert) Lemm.
Dinobryon divergens Imhof.
Asterionella sp.
Tabellaria sp.
Characium stipitatum (Bachmann) Wille.
Mougeotia sp.
Hyalotheca dissiliens (Smith) Vréb.
Micrasterias apiculata (Ehrenb.) Menegh.
M. truncata (Corda) Bréb.
Staurastrum pentacerum (Wolle) G. W. Smith.
Xanthidium antilopaeum var. *hebridarum* W. and G. S. West.

ROTIFERA (identified by G. Morley Neal)

Kellicottia longispina (Kellicott).
Polyarthra trigla Ehr.
Keratella cochlearis (Gosse).
Trichocera sp.

CLADOCERA

- Diaphanosoma brachyurum* (Liéven).
Holopedium gibberum Zaddach.
Daphnia sp.
Bosmina longispina Leydig.
Polyphemus pediculus (L.).
Acroperus harpae Baird.
Chydorus sphaericus (O.F.M.).
Acantholeberis curvirostris (O.F.M.).
Drepanothrix dentata (Eurén).
Ophryoxus gracilis Sars.

COPEPODA

- Diaptomus minutus* Lillj.
D. pygmaeus Pearse.
Mesocyclops edax (Forbes).
Macrocyclops albidus (Jurine).

COLEOPTERA (identified by W. J. Brown)

- Hydroporus undulatus* Say.
Gyrinus lugens Lec.
G. fraternus Coup.
G. dichrous Lec.
Stenelmis crenata Say.
Acryonyx variegatus Gem.

FISHES

- Salvelinus fontinalis* (Mitchill)—Eastern brook trout
Catostomus commersonni (Lacépède)—White sucker
Notemigonus crysolucas (Mitchill)—Golden shiner
Ameiurus nebulosus (LeSueur)—Brown bullhead
Anguilla rostrata (LeSueur)—American eel
Fundulus diaphanus (LeSueur)—Banded killifish
Perca flavescens (Mitchill)—Yellow perch

OBITUARY

Donald Strathearn Rawson

1905—1961



Doctor Donald Strathearn Rawson, a Member of the Fisheries Research Board of Canada, died suddenly and unexpectedly in Saskatoon on February 16, 1961.

Dr Rawson was born on May 19, 1905 near Uxbridge, Ontario, the son of Reuben Richardson and Mary (McFarlane) Rawson. He obtained his early education at Claremont and at Toronto's Harbord Collegiate Institute. Entering the University of Toronto in 1922, he received from it the degree of Bachelor of Arts in 1926, Master of Arts in 1927, and Doctor of Philosophy in 1929. His academic career was outstanding, and he was active in extra-curricular activities.

In 1932 Dr Rawson married Hildred Patton, who survives him, as do two sons and a daughter.

Dr Rawson was appointed in 1928 to the staff of the Department of Biology, University of Saskatchewan, and remained there through the remainder of his life, becoming head of the Department in 1949.

As an undergraduate and graduate student at Toronto Dr Rawson was a member of the Ontario Fisheries Research Laboratory, working first at the Lake Nipigon field station and other points in northern Ontario, later at Lake Simcoe. His Lake Simcoe studies concerned the bottom fauna of that lake and its role in fish production, providing material for both his M.A. and Ph.D. theses. These investigations, published in the University of Toronto Studies, Biological Series, were the first of his many contributions to Canadian limnology.

On arriving in Saskatchewan, Dr Rawson immediately undertook a survey of the lakes in the recently established Prince Albert National Park (1928-34). His recommendations formed the basis for rational utilization of the Park's fishing opportunities, and quickly led to requests for similar studies in other parts of western Canada. Among the surveys carried out by Dr Rawson or under his leadership may be mentioned the study of Paul, Okanagan and other lakes of interior British Columbia (1931, 1935); Clear Lake in Riding Mountain National Park, Manitoba (1935); the saline lakes of southern Saskatchewan (1938-41); lakes in the mountain parks of Alberta (1939, 1946, etc.); Lake Athabaska (1943 and 1945); Great Slave Lake (1944-47); Lac la Ronge, Reindeer Lake and other lakes in northern Saskatchewan (1948-58).

Almost without exception, these various surveys were requested with a view to obtaining a guide for best utilization of the waters concerned—either before a fishery began or because of dissatisfaction with an existing fishery. The results from this point of view have been published in such journals as the Canadian Fish Culturist, Transactions of the American Fisheries Society, the Bulletins and Journal of the Fisheries Research Board of Canada, and Fisheries Reports of the Saskatchewan Department of Natural Resources. Best known perhaps is the Great Slave Lake Survey sponsored by the Fisheries Research Board, which set the stage for commercial exploitation of that lake and for a continuing study of its fish production.

The development of fisheries management in Saskatchewan was largely influenced by Dr Rawson's investigations. His wide knowledge of the prairie

lakes made him a leader among the five members of the Royal Commission on the Fisheries of Saskatchewan in 1946-47. In recent years he encouraged the growth and development of a Provincial Fisheries Research Laboratory with headquarters at the University of Saskatchewan, which has continued the work of sound appraisal as a basis for management.

During all these studies Dr Rawson and his colleagues gave detailed attention to the physical characteristics and biological populations of the waters examined. Their publications concerning various facets of the life and environment of Lake Waskesiu, Prince Albert Park, have made that lake a classical locality among limnologists. Furthermore, broad acquaintance with different lake types in many regions stimulated Dr Rawson to publish a number of studies in which different types are compared and contrasted. These analyses are his most important scientific works for they deal with the fundamental problems of relating physical characters of morphometry, climate and geology to the production of plants and animals in lakes.

In 1944 Dr Rawson was elected a Fellow of the Royal Society of Canada. He was appointed as a member of the Fisheries Research Board in 1959, after being for many years an influential adviser of many of its activities.

Dr Rawson was a member of the American Association for the Advancement of Science, American Society of Ichthyologists and Herpetologists, American Fisheries Society, and Ecological Society of America. He was one of the founders of the Limnological Society of America (now the American Society of Limnology and Oceanography) and served as its President in 1947. At the time of his death and for many years previously he had been Canadian representative on the Council of the International Association for Theoretical and Applied Limnology. During 1936-46 he was a member of the National Committee on Fish Culture, and subsequently of the informal Canadian Committee for Freshwater Fisheries Research, of which he was President in 1951. He assisted with the organization of the Canadian Conservation Association, and later of the Canadian Society of Wildlife and Fishery Biologists, which in one of its aspects can be considered the Association's successor.

Enthusiasm for research did not prevent Dr Rawson from maintaining a steady teaching schedule at the University. He also contributed in many ways to student activities, particularly athletics, and, in later years he assumed the cares of supervising a large university department. His wife and children were his greatest pride, but he gave to his students an almost equal measure of devotion. He was intensely interested in biologists in training, and followed their subsequent careers with an active and sympathetic correspondence. His numerous graduate students occupy positions in research, teaching and fishery management throughout Canada and abroad. In recent years the planning and construction of a new biology building on the Saskatoon campus of the University of Saskatchewan took much of his time: this beautiful and functional building is an enduring monument to his labours.

Proximate Composition of Canadian Atlantic Fish

I. Variation in Composition of Different Sections of the Flesh of Atlantic Halibut (*Hippoglossus hippoglossus*)¹

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ABSTRACT

The composition of various portions of the edible flesh of Atlantic halibut (*Hippoglossus hippoglossus*) varies greatly, especially in lipid content. The muscle of the belly flap and the dark muscle along the lateral lines in the upper and lower sides have a high lipid content, 2.4 to 9.7%, with correspondingly lower moisture content, about 68 to 75%, and a slightly low protein content, about 16.3 to 19% (protein N $\times$ 6.25) in comparison with the light meat. The latter, which makes up the larger part of the edible tissue, nearly 90%, ranges from 0.9 to 1.4% lipid, 75 to 77% moisture and 17.5 to 20.3% protein. These values are almost identical to those for Pacific halibut (*Hippoglossus stenolepis*). Non-protein nitrogenous extractives are also lower in the white meat.

The figures most often quoted in nutritional tables for the lipid content of halibut (5 to 6%) are probably much too high for the portions usually eaten, which average about 1.2% for the white meat, and about 1.5% if the dark meat is included.

INTRODUCTION

IT HAS BEEN RECOGNIZED for many years that the composition of the edible portion of the flesh of fish and shellfish varies with many factors, among them, size, sex and stage of sexual maturity, season and place of catching. Atwater (1892) concluded that there was some seasonal influence in certain species, as during the spawning migration of salmon. Clark and Almy (1918) found large variations in fat content with feeding activity and with the spawning cycle, particularly in shad. Johnstone (1918) studied the maturation of herring showing the accompanying large changes in fat and moisture. Thus, abundance of food, spawning cycle, spawning migrations and age influence the composition of any particular species. The effect of these factors has been reviewed recently by Stansby (1954) and Vinogradov (1953).

Tables of proximate composition of the edible portion are given in several reference works, e.g. McCance and Widdowson (1940), Watt and Merrill (1950), but usually few data are given on the number of samples analyzed, and indeed it is known that many quoted figures are based on single determinations.

It is only recently that the variation in different parts of the muscle from an individual fish has been emphasized (Brandes and Dietrich, 1953; Thurston, 1958; Thurston and MacMaster, 1960) although it was recognized by Clark and Clough (1926) in certain fatty species.

¹Received for publication January 24, 1961.

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The major constituents are water, fat, and protein, with ash and certain extractives including non-protein nitrogenous compounds making up lesser amounts. In general, the moisture content is about 80% with reduced levels in the more fatty species. The protein content has been found to remain relatively constant except under conditions of advanced starvation, in spite of great variations in fat content. This is usually expressed by the rule that the sum of the percentages of water and fat is nearly constant, about 81% (Clark and Almy, 1918). For instance, in herring (*Clupea harengus*) Reay *et al.* (1943) found that the percentage of water was equal to $80.2 - (0.96 \times \text{percentage of fat})$.

The ash content usually varies between 1 and 1.5%. Higher values usually indicate inclusion of bone or sometimes brining prior to sampling.

The procedures often used for fat and lipid determination have yielded results dependent on the solvent and procedure (Love *et al.*, 1959). The development of two apparently more reproducible procedures should lead to the resolution of this difficulty (Damberg, 1956; Bligh and Dyer, 1959).

There is a real scarcity of data on the composition of the Canadian Atlantic species, its variation in different parts of the fillet or individual fish, and the effect of the various processing and preservation procedures. It is evident that such data are of interest to dietitians concerned with nutritional values of fish and sometimes with levels of fat and salt in the diet, and to processing engineers who deal with the varying yields of primary products, with the various by-products in all seasons and with fish from various sources.

A study was thus undertaken of some Atlantic species of fish and shellfish, of which this report on Atlantic halibut (*Hippoglossus hippoglossus*) is the first part.

METHODS

1. SAMPLING

In small halibut (chicken halibut) a cross-sectional slice was taken from the thickest part of the fish, following the practice of Love (1958, 1960) who used the region from myotome 7 to 14 which in cod is about one-quarter along the length of the fillet from the anterior end. This was designated A, and another was taken from the tail section about half-way between the vent and the end of the fillet, designated B.

Another sample was taken from the thin section of muscle around the abdominal cavity, designated the belly flap, C.

In large halibut, steaks were obtained from about the same regions as A and B above, but in this instance, three samples were cut from each steak: the upper one-eighth portion of the steak, D; the lower one-eighth portion, F; and the central portion, E. (See diagram, Fig. 1.) Thus the fatty layer running along the centre of each side was removed, leaving the relatively lean white muscle in the central part (E). Somewhat the same procedure with some additional sampling was used by Thurston and MacMaster (1960), published after this work was completed. Thus samples D and F contained a small proportion of white meat in addition to the fatty layer. The skin and bones were carefully removed in all

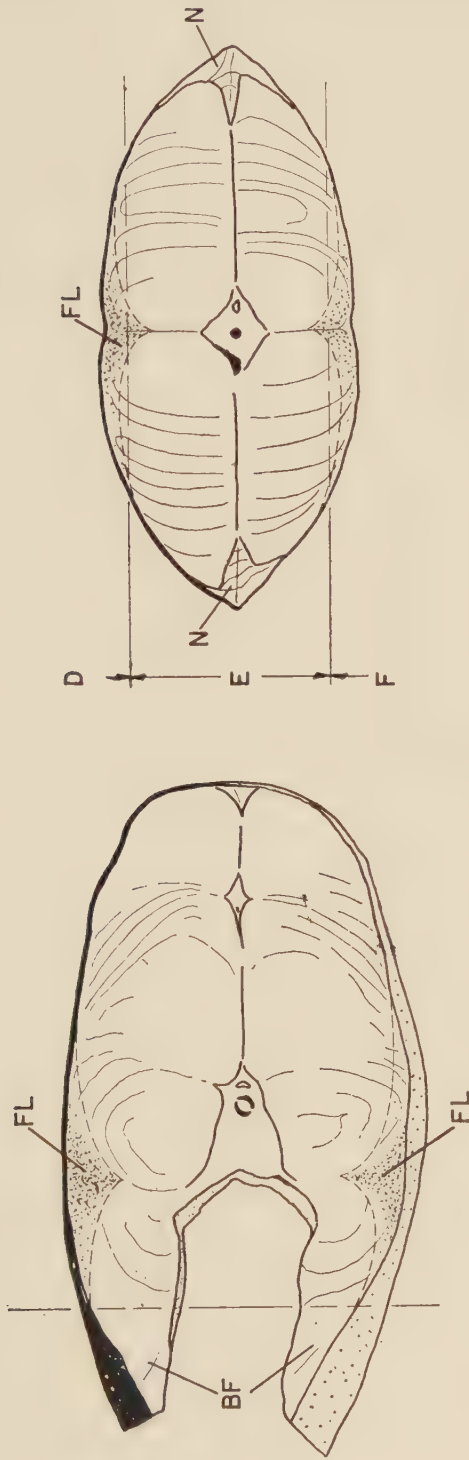


FIG. 1. Diagram of halibut steak showing sampling locations:
FL—Lateral dark muscle;
BF—Belly flap;
D—Upper section of tail steak;
F—Lower section of tail steak;
E—Central section of tail steak;
N—"Notch" meat around dorsal and ventral fins.

samples. The samples were then comminuted with a knife, well mixed, and portions weighed immediately for the various analyses.

The halibut were obtained iced fresh from a local plant. They were caught by shore boats in local waters and were less than 24 hours in ice. Dates of landing are given in the Tables. In one instance steaks from a large halibut were frozen and stored in polyethylene bags at -23°C for a period of 2 months.

To determine the relative proportion of white meat, etc., frozen steaks from a medium halibut, about 100 lb, were obtained. These were frozen samples of unknown age but in good condition. The skin, dark muscle, white muscle and bone which readily separated on partial thawing were carefully dissected out, weighed and analyzed. In addition, the "notches" or wedges of whitish, jelly-like tissue, N in Fig. 1, in which the dorsal and ventral fins were embedded, were also separated.

Two samples of "chalky" halibut, which were landed at a local fish plant from a trawler, were examined. The flesh appeared to be quite opaque, flaked apart easily, was softened and very wet. The light meat only from a cross-sectional "steak" cut from the thickest part of each fish was analyzed.

2. ANALYTICAL METHODS

Water. Samples of 20 to 50 g were dried to constant weight at 105°C , usually for 24 to 48 hr.

Lipid. Samples of 50 g were extracted according to the chloroform-methanol phase separation procedure of Bligh and Dyer (1959).

Ash. Samples were ignited to constant weight at 550°C .

Total nitrogen (TN). The Kjeldahl-Gunning-Arnold method (A.O.A.C., 1955) was employed, using 2- to 5-g samples.

Non-protein nitrogen (NPN). A 25-g sample was triturated with trichloroacetic acid of a final concentration of 5%, and nitrogen was determined in the filtrate using a micro-Kjeldahl procedure (Dyer *et al.*, 1950).

Certain non-protein nitrogenous constituents were also determined to indicate whether these constituents varied in the same manner as the major constituents. The content of trimethylamine (TMA) and ammonia, and the tyrosine value, also served as a check on the "freshness" of the samples.

TMA. Aliquots of the trichloroacetic acid filtrate were subjected to the colorimetric procedure of Dyer (1959).

Trimethylamine oxide (TMAO). Following reduction to TMA (Dyer *et al.*, 1952) the latter was estimated as above.

Tyrosine. The tyrosine value was determined according to the procedure of Wood *et al.* (1942).

Ammonia. One gram of tissue was triturated with 200 ml water and ammonia estimated in the filtrate with Nessler's reagent.

Free fatty acid (FFA) The procedure of Bligh *et al.* (1957) was employed.

Salt-extractable protein N (SPN) and actomyosin N (AM). Samples of 22.5 g were blended with 0.85*M* NaCl (0.003*M* bicarbonate buffer) for 2.5 minutes (Dyer *et al.*, 1950).

RESULTS AND DISCUSSION

In chicken halibut, about $2\frac{1}{2}$ ft in length, differences appear in moisture and lipid content between samples taken from the thick section and from the tail (Table I). The thick section averages 3.1% lipid, in comparison with only 1.2% in the section toward the tail, while the belly section has much more, 4.8%. As expected, the moisture content of the latter is less than in the cross-section samples. It is apparent that some fatty meat from the belly section and from the fatty strip running down each side is being included in the cross-section samples. Consequently in subsequent sampling these fatty tissues were removed, leaving the apparently fatty-tissue-free central section. The belly flap has a slightly lower protein content, 15.6% expressed as protein nitrogen $\times 6.25$, with a higher proportion of total nitrogen present as NPN (Table II). However, the TMAO level is the same for all sections.

The results for the three samples of large halibut show that a large part of the fat is concentrated along the "lateral lines". The upper section (D) contains from 2.4 to 9.1% lipid, the lower (F) 3 to 9.9%, while the central section has only 0.9 to 1.4%. Moisture contents are correspondingly less in the more fatty sections where NPN is higher and protein lower. Again there is little change in TMAO. The constancy of the TMAO content is interesting since Shewan (1951) indicates that the dark muscle of herring and tunny contains only half as much as the rest of the skeletal muscle. Tyrosine values are higher in the fatty layers, probably indicating more soluble peptides and amino acids.

For convenient comparison with earlier literature, the sum of moisture, ash, lipid, and crude protein (TN $\times 6.25$) is given in Table I. Since at least some of the NPN may be used for protein synthesis in metabolism, this method of calculating results may have some usefulness, e.g. for dietetic purposes, especially since it is the most commonly used procedure. (For a more complete discussion, see Vinogradov (1953) and Love (1957).)

The sum of moisture, lipid, ash, and protein nitrogen $\times 6.25$ is also given. It does not include the non-protein nitrogenous compounds or other extractives, and therefore the sum usually adds to about 97%. This was partially allowed for in the earlier literature by calculating protein as total nitrogen multiplied by the factor 6.25. It seems better to calculate true protein (assuming nitrogen content of muscle protein is 16.0%), and the differences between the sum obtained and 100 will then give a rough measure of the extractives, which, from the average of all values given, is about 2.5%. In cod, the nitrogenous extractives consist mainly of creatine, trimethylamine oxide, taurine, anserine, purine and pyrimidine derivatives (Shewan and Jones, 1957). For the composition given by these authors, the average nitrogen content of these nitrogenous extractives is 21%. Since the nitrogenous extractives from cod and the flatfishes are quite similar

TABLE I. Proximate composition—percent wet weight.

Data		Water	Lipid	Ash	TN	Crude protein ³	Total A ⁴	NPN	PN ⁵	Protein ⁶	Total B ⁷
Chicken halibut (Feb. 9, 1959) 2 fish	A1	74.5	3.1	1.35	3.38	21.1	100.0	0.57	2.81	17.5	96.5
	A2	76.1		1.38	3.37	21.1	101.7	0.57	2.80	17.5	98.1
	B1	77.2	1.2	1.50	3.38	21.1	101.0	0.70	2.68	16.8	96.7
	B2	76.9		1.55	3.36	21.0	100.6	0.71	2.65	16.6	96.3
	C1}	75.9	4.8	1.53	3.28	20.5	102.7	0.79	2.49	15.6	97.8
	C2}										
Large halibut (June 6, 1959) Tail steak	D	70.4	9.1	1.20	3.43	21.4	102.1	0.55	2.88	18.0	98.7
	E	76.2	1.4	1.25	3.66	22.9	101.7	0.43	3.24	20.2	99.1
	F	69.2	9.4	1.15	3.41	21.3	101.0	0.54	2.88	18.0	97.8
Large halibut (July 24, 1959) Steak from back of vent	D	75.5	2.4	1.40	3.31	20.7	100.0	0.71	2.60	16.3	95.6
	E	77.6	0.9	1.30	3.26	20.4	100.2	0.46	2.80	17.5	97.3
	F	74.1	3.0	1.30	3.47	21.7	100.1	0.73	2.74	17.1	95.5
Large halibut (Apr. 20, 1959) Steak from back of vent frozen and stored 2 mo. at -23°C	D	72.4	6.9	1.30	3.49	21.8	102.4	0.48	3.01	18.8	99.4
	E	75.1	1.2	1.45	3.63	22.7	100.4	0.38	3.25	20.3	98.1
	F	68.0	9.9	1.00	3.41	21.3	100.2	0.55	2.86	17.9	96.8
Chalky halibut Light meat only from Section A	A1	78.8	1.1	1.40	3.16	19.7	101.0	0.51	2.65	16.6	97.9
	A2	76.4	0.9	1.30	3.56	22.2	100.8	0.51	3.05	19.0	97.7
Average E (3) Average D + F		76.3	1.2	1.33	3.51	21.9	...	0.42	3.09	19.3	...
		71.6	6.8	1.27	3.42	21.4	...	0.59	2.83	17.7	...

³Crude protein—TN × 6.25.
⁴Total A—Sum of water, lipid, ash and crude protein.
⁵PN—Protein N
⁶Protein—PN × 6.25.
⁷Total B—Sum of water, lipid, ash and protein.

TABLE II. Non-protein nitrogenous and protein constituents.

Data	NPN		NPN	TMA	TMAO	NH ₃	Tyr.	SPN ⁸	AM ⁹	Alb ¹⁰	FFA ¹¹
	% wet weight		%TN	mg N/100 g					% TPN ¹²		% lipid
Chicken halibut (Feb. 9, 1959) 2 fish	A1	0.57	16.8	0.24	46	...	...	...	...	...	2.7
	A2	0.57	16.9	0.25	47	...	...	...	...	...	...
	B1	0.70	20.7	0.24	46	...	...	...	...	...	4
	B2	0.71	21.1	0.21	47	...	...	...	...	...	...
	C1 } C2 }	0.79	24.0	0.24	46	...	...	...	...	...	1
Large halibut (June 6, 1959) Tail steak	D	0.55	16.0	1.9	56	14	38	60	42	18	0.6
	E	0.43	11.5	0.4	59	8	18	76	53	22	1.6
	F	0.53	15.5	0.6	58	14	56	65	42	23	0.4
Large halibut (July 24, 1959) Steak from back of vent	D	0.71	21.4	2.2	57	14	49	81	55	26	2
	E	0.46	14.1	1.3	63	17	24	86	62	24	4
	F	0.73	21.0	2.2	58	17	87	71	47	24	1.5
Large halibut (Apr. 20, 1959) Steak from back of vent frozen and stored 2 mo. at -23°C	D	0.48	13.8	0.6	54	9	29	71	49	22	3
	E	0.38	10.3	0.4	57	12	17	78	54	24	9
	F	0.55	16.1	0.5	50	12	46	68	45	23	3
Chalky halibut (May 1, 1959)	A1	0.51	16.2	0.7	68	...	...	82	62	20	7
Light meat only from Section A	A2	0.51	14.3	0.8	65	...	...	55	40	15	12
Average E (3)		0.42	12.0	0.7	60	...	...	80	...	23	...
Average D + F		0.59	17.3	1.3	55	...	...	70	...	23	...

⁸TPN—Total protein N.⁹SPN—Salt-extractable protein N.¹⁰AM—Actomyosin N.¹¹Alb—Albumin N.¹²FFA—Free fatty acid.

both in kind (Shewan, 1955), and in amount (Shewan, 1951), we can calculate that the total nitrogenous extractives in the white flesh of the halibut will be approximately 2.0% using a NPN content of 0.42%

Allowing for a smaller amount of non-nitrogenous extractives, the total proximate composition is thus close to 100%.

The average values for the three central (E) sections and combined upper and lower (D and F) sections are shown at the bottom of the Tables and illustrate the differences between the fatty tissue and the white muscle.

It is interesting to compare these averages with the data of Thurston and MacMaster (1960). For small and large specimens of the closely related Pacific halibut (*Hippoglossus stenolepis*), the average of the nape, central and tail sections (which showed almost no differences between them), excluding the belly flaps and dark muscle, was 77.9% moisture, 0.7% lipid, 1.39% ash, and 21.2% crude protein. The corresponding averages obtained in the present work, sample E, were 76.3, 1.2, 1.33 and 22.0% respectively. This agreement appears to be remarkable indeed. The higher average lipid content could be due to the different procedure used for its estimation. These authors also found a high lipid content averaging 7% in the fatty brownish layer which corresponds with the high value, 6.8%, in the D and F samples in the present work.

Several authors quote data for the composition of the muscle tissue of halibut (mainly *Hippoglossus hippoglossus*) e.g.:

	Water	Fat	Crude protein	Ash
Reay <i>et al.</i> (1943)	75.4-79.0	0.5-9.6	18-18.8	...
Taarland <i>et al.</i> (1958)	74.5	6.0	18	1.0
Watt and Merrill (1950)	75.4	5.2	18.6	1.0
Vinogradov (1953)	74.5-77.6	...	18.1-20.5	0.7-1.1

It will be seen that with the exception of fat, these values are close to the present results, although ash and crude protein are slightly lower.

The figures quoted for fat content are rather high, and are close to the values obtained for the fatty tissue in the present work. Perhaps nutritionists and dietitians would be well advised to use the much lower values of the white meat, about 1.2%, since this is the portion which will be eaten by most people, the more fatty portions often being discarded prior to serving, or left on the plate.

The proportion of the total nitrogen contributed by NPN is remarkably higher for the fatty upper and lower sections, 17.3%, than for the central section, 12%. NPN was not determined by Thurston and MacMaster. Lukton and Olcott (1958) give a NPN content of 0.38% for the Pacific halibut, very close to the present results.

The proportion of the edible flesh in the steaks from both the thick section of the fish and from the tail section was the same, 91.0 and 90.5% respectively (Table III). The skin was 3.4% in both cases, bone constituting the remainder. Of the edible portion the white meat constituted about 90%, the dark or fatty layered meat 6 to 7%, and the "notch" meat 3.6 to 5.2%.

TABLE III. Proportion of skin, bone and edible meat in halibut steaks (frozen halibut steaks, December 1960).

	Steak from thickest section of fish (Section A) (Total wt. 735 g)	Steak from tail section (Section B) (Total wt. 408 g)
<i>Proportion of total weight represented by:</i>		
Skin	3.4	3.4
Bones	5.6	6.1
Edible portion	91.0	90.5
<i>Proportion of edible weight represented by:</i>		
White meat	90.2	87.4
Dark meat (FL)	6.2	7.4
Notch meat	3.6	5.2

The analytical data for these portions (Table IV) agree closely with the results already reported. The white meat contains only 0.74 to 1.14% lipid as compared to 3.9 to 8.5% for the dark meat. The steaks were not taken from the same fish so no comparison of the tail and middle steaks can be made in this case. If the average fat of the edible portion is calculated, taking into account the lipid content and the proportion of each type of meat, the middle steak averages 1.7%, and the tail steak, 1.3%. These data support the conclusion that the usual fat content quoted for halibut is much too high.

TABLE IV. Composition of white and dark meat of halibut steak (from samples used in Table III).

	Water	Lipid	TN	Crude protein	NPN	PN	Protein	NPN % TN	TMA	TMAO
	% wet weight								mg	N/100 g
Middle steak—A										
White meat	77.2	1.14	3.23	20.1	0.46	2.79	17.3	14.2	0.2	69
Dark meat	71.7	8.5	3.00	18.8	0.55	2.45	15.3	18.3	1.3	54
Tail steak—B										
White meat	79.9	0.74	3.04	19.0	0.43	2.61	16.3	14.1	0.2	70
Dark meat	76.9	3.9	2.88	18.0	0.63	2.25	14.1	21.9	2.6	53
Notch meat	76.6	7.6								

NPN is considerably higher in the dark meat, while on the other hand the TMAO content is about 23% lower. The lipid content of the "notch" meat is high, 7.6%, even though this portion is almost colourless to white, being non-pigmented in sharp contrast to the brownish fatty layer along the lateral lines. The sample analyzed was lower in fat than the corresponding portion of the Pacific halibut which is reported to contain about 40% fat (Thurston and MacMaster, 1960).

In the chalky halibut the lipid content is normal, 0.9 to 1.1%. Moisture and protein are normal in one sample, although protein is considerably lower in the other, only 16.6%.

The protein extractable in neutral 0.85M sodium chloride solution was determined on several of the samples (Table II). The E samples average approximately 80% (as percentage of total protein nitrogen). This value is rather low when compared to most values for fish flesh, and probably more could be obtained by more exhaustive extraction. However, on a comparative basis, that extracted from the D and F samples is considerably lower, averaging 70%. The albumin or water-soluble protein, that fraction remaining after precipitation of the actomyosin from the salt extracts by dilution to an ionic strength of 0.05, averages 23% in both instances. The chalky halibut sample (A1), with rather low protein N content (2.65%), gives similar values, but the other (A2), containing 3.05% protein N, yields only 55% SPN and the albumin is also low, only 15%. The significance of these results is unknown, though there may be some relation to the spawning cycle when the depot fat and some of the body protein may be used to supply energy and protein to the rapidly increasing egg mass during maturation, in which case some of the protein may be replaced by water. In jellied plaice, Templeman and Andrews (1956) found much higher moisture than the normal, and much lower total protein and extractable actomyosin, while the proportion of unextractable or stroma protein was increased. The latter would result if muscle protein was depleted. The chalky halibut described here seems to be different from Pacific chalky halibut which appear to contain less water, more fat, and usually less protein (Bailey, 1950, 1951).

The present results show the great variation in lipid content in Atlantic halibut between the white meat of the central muscle, the dark meat along the sides, and the muscle of the belly flap. They are in substantial agreement with the extensive data of Thurston and MacMaster on the Pacific halibut.

ACKNOWLEDGMENT

The authors wish to thank Mr H. E. Power for drawing the diagrams.

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Proximate Composition of Canadian Atlantic Fish

II. Mackerel, Tuna and Swordfish¹

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ABSTRACT

Mackerel, tuna and swordfish (order Acanthopteri) have a prominent red or dark brown fatty lateral-line tissue which, in the samples analyzed, had a lipid content varying from 6% in swordfish to 22% in mackerel. A white blubber or layer of fat tissue, almost two-thirds lipid, may also be present beneath the skin. The white meat was also fatty, from 2% in swordfish to 8% in tuna. The belly-flap muscle of mackerel contained from about 20 to 40% fat. Protein, ash and moisture percentages were lower in the fatty tissue, showing that fat replaces some protein as well as water. Non-protein nitrogen averaged 20% of the total nitrogen, higher than in halibut and the cod family. In tuna and mackerel the protein content was 19% in the white meat and 14% in the brown lateral-line tissue, similar to halibut but higher than in the cod family.

INTRODUCTION

IN PART I OF THIS SERIES (Mannan *et al.*, 1961) considerable differences in composition between various sections of the flesh of Atlantic halibut (*Hippoglossus hippoglossus*) were noted.

Some variations found in the composition of the various portions of the flesh of mackerel (*Scomber scombrus*), tuna (*Thunnus thynnus*) and swordfish (*Xiphias gladius*), all of the order Acanthopteri, are reported here. These species are characterized by the presence of a very prominent lateral-line muscle, usually of a red or dark brown colour. The importance of considering this section of the flesh separately is pointed out by Hamoir (1953a), who also shows that myoglobin is responsible for the red colour (1953b). This muscle in mackerel, herring and halibut has a very high fat content, 27 to 29% (Braekkan, 1956). Love *et al.* (1959) summarize the few data available on the composition of the dark meat of several fish species, showing that this part of the musculature is considerably different in some respects from the white muscle.

EXPERIMENTAL

SAMPLING AND SOURCE OF SPECIMENS

The iced fish were landed from small boats at a local fish plant, and were almost always less than 24 hr out of the water when sampled.

The fall mackerel samples were frozen and stored in polyethylene bags at -23°C for 3 months. As described in Part 1 of this series, cross-sectional samples were taken of the edible flesh near the thickest part of the fish, A, toward

¹Received for publication March 2, 1961.

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the tail, B, and of the flesh of the belly flap, C. In the June 8 samples, the dark brown muscle (DB) along the lateral line (FL, fig. 1 in Part 1) was analyzed separately. The flesh of six specimens was minced and well mixed for these samples. In tuna samples of the pink (white) meat (P), the whitish fatty meat which was layered somewhat like bacon (F), and the thick layer of blubber under the skin were taken.

In the swordfish the white (A) and dark (DB) meat from steaks near the middle section were sampled.

The analytical procedures used are given in Part 1 of this series. All values given in Table I for total nitrogen (TN), non-protein nitrogen (NPN), trimethylamine oxide (TMAO), trimethylamine (TMA), salt-extractable protein nitrogen (SPN) and actomyosin nitrogen (AM) are the average of duplicate determinations.

RESULTS

These species have high fat levels in the muscle tissue. The fat fall mackerel specimens have lower lipid in the tail section (12.6%) than in the thick part (18.8%), while the fat in the belly flap is much higher, 37.2%. The spring mackerel (June 8) with a much lower total fat content still retains 18 to 19% fat in the belly flap, 4 to 6 times the content of the white flesh. The dark brown muscle of the lateral line comprises 1/7 of the weight of the edible flesh. The proportion of dark muscle is greater in the tail section, 27%, as compared to 11% in the thick section (Table II). The dark muscle also has a high fat content,

TABLE II. Proportion of skin, bone, and edible meat in steaks of fall mackerel. Fish 34 cm long.

	Steak from thickest part of fish (Section A) (Total wt. 155 g)	Steak from tail section (Section B) (Total wt. 68 g)
<i>Proportion of total weight represented by:</i>	%	%
Skin	3.0	2.7
Bone	5.6	10.7
Edible portion	91.4	86.6
<i>Proportion of edible portion represented by:</i>		
White meat	71	73
Dark layer	11.3	27
Belly flap	18.5	0

about 22%. Moisture, ash and protein are lower in the brown fatty lateral line and belly flap tissue, while TMAO is higher in the brown layer.

Tuna has rather more fat in the pink muscle, 4 to 8% (mackerel, 3.2 to 4.9%), while the thick layer of whitish fatty meat is much fattier, 34% (mackerel 18.8%). A sample of blubber from near the skin shows 64% fat. Protein levels are considerably lower in the fatty tissues.

The swordfish samples are less fatty, the levels averaging 2 and 6% in the white and dark meat respectively. The NPN constituents are almost identical but protein, ash and moisture are lower in the dark meat.

The NPN levels in this group are considerably higher than in the halibut and cod families, averaging about 20% of the total nitrogen. In swordfish, a much lower value of 0.24% NPN is reported by Lukton and Olcott (1958). The TMAO levels are quite low in this group in agreement with previous work (Groninger, 1959).

The protein (protein N $\times$ 6.25) of the white meat, 16.5 to 18.8%, is similar to halibut and somewhat higher than in the cod family. The fat tissue, however, contains only about 14%. The protein extractability in salt solution is comparable to the other groups, varying from 90 to 97% extractable protein nitrogen, with slightly lower values in the dark brown muscle of the mackerel. The albumin fraction is considerably higher in the tuna, about 32% of the protein as compared to about 23% in other fish species.

The free fatty acid (FFA) of the extracted fat is very low, probably because of the high fat levels. Even in mackerel frozen at -10°F for 3 months, there was no appreciable hydrolysis of the fat.

In Table III some published values for the proximate composition of these species are tabulated. Apart from wide variations in moisture and especially lipid content associated with seasonal changes, the protein and ash are quite constant and consistent with our results when the variations due to sampling such a mixture of lean and of fatty tissue is considered. The distinguishing characteristic of this group of fishes is the presence of a variable and often large

TABLE III. Proximate composition of edible flesh of mackerel, tuna and swordfish.

Source	Water	Lipid	Ash	Crude protein (total nitrogen $\times$ 6.25)
	Percentage of wet weight			
Mackerel (<i>Scomber scombrus</i>)				
Watt and Merrill (1950)	68.1	12.0	1.2	18.7
Vinogradov (1953), (Av. of 11)	70.0	...	1.36	19.6
Range:	64.4-73.1	...	0.9-1.85	15.6-24
Braekkan and Probst (1953)	74.0	5.1	1.3	19.6
Taarland <i>et al.</i> (1958)—Spring	74.3	5.4	1.5	18.6
—Fall	60	20.2	1.3	18.5
Tuna (<i>Thunnus thynnus</i>)				
Dill (1921)	65-73	1-9	1.3-1.4	24-25
Vinogradov (1953), (Av. of 3)	70.2	...	1.3	26.5
Range:	69.1-70.8	...	1.25-1.4	26.5
Taarland <i>et al.</i> (1958)	66.0	9.9	1.1	24
Swordfish (<i>Xiphias gladius</i>)				
Lopez-Matas and Fellers (1948)	76.6	3.1	1.0	18.9
Watt and Merrill (1950)	75.8	4.0	1.3	19.2
Vinogradov (1953), (Av. of 4)	76.6	...	1.4	19.8
Range:	75.3-77.5	...	1.2-1.5	18-20.5

proportion of the brown fatty lateral-line tissue. In some species there is present a layer of depot fat or blubber below the skin which is about two-thirds fat. The latter may correspond to the white fatty "notch" meat in halibut. The contrast with the lean fishes of the cod family is striking, lipid being much higher, and it was found that the protein and NPN contents are also greater. This higher content of NPN contributes to and enhances the flavour of these species (Shewan, 1951).

The large differences in the composition of the various tissues in these species make sampling for detection of storage changes and accurate determination of composition for dietetic and other purposes extremely difficult.

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The Amino Acid Composition of Cod Tropomyosin¹

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ABSTRACT

The amino acid composition of cod tropomyosin was determined. Most analyses were done by chromatography on columns of ion-exchange resins (Moore and Stein technique); tryptophan and cystine were determined chemically.

The results are compared with published values for tropomyosins from other sources. Similarities and differences between the various tropomyosins are discussed. The probable number of residues of each of the amino acids in the tropomyosin molecule is calculated.

INTRODUCTION

FOLLOWING BAILEY'S (1946, 1948) discovery of tropomyosin as a protein component of rabbit skeletal muscle, many have studied the chemical and physical properties of this protein. The earlier investigations (Astbury, 1947; Bailey, 1948; Bailey *et al.*, 1948; Astbury *et al.*, 1948; Adair *et al.*, 1949) were mainly concerned with tropomyosin from rabbit muscle. Hamoir's (1951) was the first publication dealing with tropomyosin from another species of animal; it described the isolation of the protein from carp muscle. Since then, tropomyosins from many additional animals have been studied: squid (Yoshimura, 1955); pig, duck, prawn, cuttlefish (Tsao *et al.*, 1955); *Pinna nobilis* (Bailey, 1956); octopus, oyster (Bailey, 1957); clam (Laki, 1957); cow, man (Kominz *et al.*, 1957c); lobster, whelk, lugworm, earthworm (Kominz *et al.*, 1957a, b); haddock (Kubo, 1957); scallop (Rüegg, 1958); lamprey, frog (Saad *et al.*, 1959); and cod (Dingle and Odense, 1959).

It now appears that at least two tropomyosins exist, commonly referred to as "vertebrate" and "invertebrate" types, with different solubilities in ammonium sulphate solutions (Bailey, 1948, 1956, 1957; Bailey and Rüegg, 1960; Kominz *et al.*, 1957b, 1957c), which may be distinguished chemically by their amino acid compositions. These proteins, designated Tropomyosin-A (invertebrate) and Tropomyosin-B (vertebrate = Bailey's rabbit tropomyosin) by Kominz *et al.*, may be basic units used in the formation of myosin, a contractile protein of muscle fibrils (Bailey, 1948; Kominz *et al.*, 1954, 1957b; Yoshimura, 1955; Laki, 1957a).

However, the situation may be much more complicated since the distinction between types A and B was only made on the basis of major differences in amino acid composition, involving primarily glutamic acid, lysine, arginine, and amide residues in the tropomyosin molecule. Some differences of a lesser nature involving other amino acids, e.g. tyrosine and methionine, appear to be class

¹Received for publication February 8, 1961.

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specific, and it has been suggested by Laki's group (Kominz *et al.*, 1957b) that differences specific to species might be found if a sufficiently thorough investigation were performed.

Undoubtedly, knowledge of the sequence in which the amino acid residues occur in the tropomyosin molecule would be of great value in helping to classify this protein, and make it possible to explain some of its physical, chemical, and biochemical properties or even its possible role in muscle contraction.

For this reason, an analytical study of cod tropomyosin was begun some years ago, with the intention to resolve the sequence of amino acids in its molecule. The choice of cod muscle as the starting material in this study was simply made because of this Station's general interest in cod muscle proteins.

This paper deals with the preparation of cod tropomyosin, with the proximate analysis of the protein and with the determination of its amino acid composition.

MATERIALS

Tropomyosin. Two preparations of tropomyosin were made, the first a purified product which was prepared in bulk (about 100 g), and the second a highly purified material³ of which only 500 mg was obtained. The starting material for both preparations was filets of fresh Atlantic cod (*Gadus callarias*).

The bulk preparation was made in batches of 10 to 15 g each following the alcohol precipitation procedure of Dingle and Odense (1959), which was slightly modified to adapt it to the handling of a larger quantity of filets per batch (about 4000 g). These modifications included: the use of a filter press rather than a centrifuge in the first solvent-treatment stages, the use of a continuous Webcel dialyser for all dialyses, and final precipitation of the tropomyosin with acetic acid followed by washing with alcohol and ether.

A preliminary check on the purity of each batch was the determination of tryptophan. When there was less than 0.04% (dry basis), the preparation was subjected to further tests of purity by means of moving-boundary electrophoresis⁴. The batch was accepted for use whenever the purity of the protein was 95 to 100%. Acceptable preparations were combined and thoroughly mixed; the mixture, "bulk tropomyosin", was used in the studies reported below. The electrophoretic pattern of a representative batch is given in Fig. 1.

The descending side of the pattern showed the presence of one protein component other than tropomyosin whereas the ascending side indicated that a second impurity was present. Planimetry showed that tropomyosin constituted 96% of the total protein and the impurities 4%. One of these impurities was probably actin. It was assumed that the amino acid compositions of the two impurities would be sufficiently similar to permit calculations on the basis of actin only. This appeared justifiable because the correction for total impurities is small.

³Prepared by Dr P. H. Odense of this Station.

⁴Carried out by Dr J. R. Dingle of this Station, using Spinco Model H apparatus.

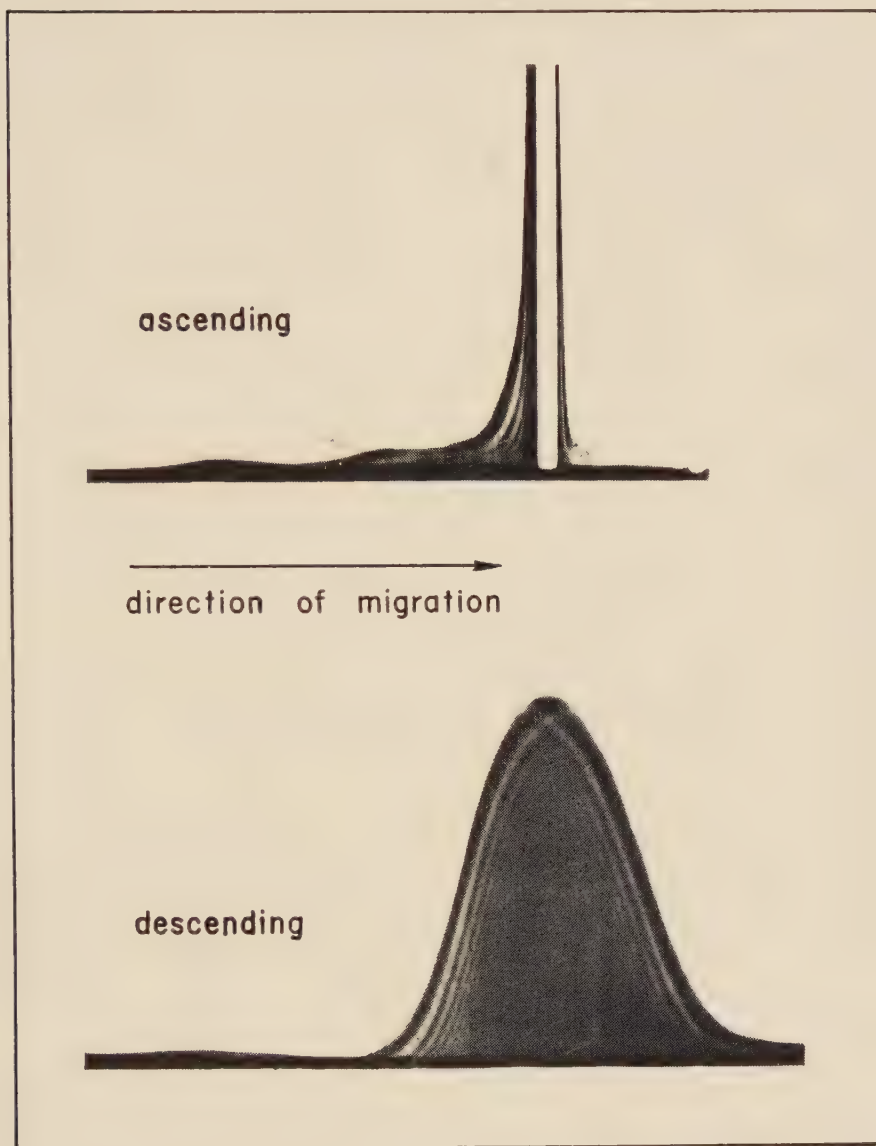


FIG. 1. Electrophoretic pattern of cod tropomyosin (bulk preparation).
Solvent: 0.10M KCl + K phosphate, $\Gamma/2 = 0.15$, pH 7.
Temperature: 1.2°C.
Duration of electrophoresis: 309 min.
Field strength: 4.4 volts/cm; current: 30 milliamperes.
Concentration: 0.862 mg N/ml.
Migration from left to right.

Highly purified tropomyosin was prepared following Bailey's (1948) procedure. Three consecutive steps of purification by precipitation with ammonium sulphate were employed; the final protein was precipitated with ammonium sulphate concentrations between 1.83 and 2.84 molar (45 and 70% saturation at 20°C). This product was electrophoretically homogeneous; the purity of the protein was probably better than 99%.

Resins and chemicals for use with the Beckman/Spinco Amino Acid Analyzer were of the quality specified in the Instruction Manual (Spackman, 1960).

Carboxypeptidase. Proteinase-free preparation as obtained from Nutritional Biochemicals, Inc., Cleveland, Ohio.

Zeokarb 225. Obtained as Permutit Q from the Permutit Company, New York.

METHODS

Moisture. The weight lost by preparations kept at 105°C for 24 hr, followed by 1 hr at room temperature in a vacuum desiccator with phosphorus pentoxide as the drying agent.

Ash. Residue at 525°C; method 29.13 A.O.A.C. (1955).

Nitrogen. Micro-Kjeldahl; selenium catalyst.

Tryptophan. Spies and Chambers (1949).

Sulphur. Oxidation in Parr bomb with sodium peroxide, followed by gravimetric determination of sulphate as barium sulphate.

Cystine + cysteine. Block and Bolling's (1951) adaptation of the Winterstein-Folin reaction.

Nucleic acid. From difference in absorbance at 261 m μ of solutions of tropomyosin before and after treatment with perchloric acid. Calculation following Dingle and Odense (1959). Results are expressed as nucleic acid, although the compounds present in the tropomyosin preparations may have been smaller (non-dialysable) polynucleotides or polynucleosides.

N-terminal amino acids. Sanger's fluorodinitrobenzene procedure (see Fraenkel-Conrat *et al.*, 1955) followed by paper chromatography.

C-terminal amino acids. Digestion with carboxypeptidase; isolation of liberated amino acids with Zeokarb 225 and identification of these acids by paper chromatography (see Fraenkel-Conrat *et al.*, 1955).

Amino acids. Ion-exchange chromatography of acid hydrolysates of tropomyosin following Spackman *et al.* (1958) using the Beckman Spinco Automatic Amino Acid Analyzer.

Hydrolysis. Samples, approximately 250 mg each, were refluxed with 5 ml constant boiling hydrochloric acid for 22 hr. Acid was removed by distillation under reduced pressure (repeated three times after addition of water). The practically acid-free residue was taken up in citrate buffer pH 2.2 ("sample-diluent" buffer containing thiodiglycol, BRIJ and octanoic acid; see Spackman,

1960) and made to the volume required to obtain a nitrogen concentration of approximately 0.150 mg/ml. Two millilitres of this solution was used on each column.

Corrections for hydrolytic losses. Determined by analysis of 6-, 12-, 22-, 40-, and 72-hr hydrolysates of tropomyosin. The factors applied to results of 22-hr hydrolysates were: threonine 1.10; serine 1.06; valine 1.03; and isoleucine 1.03. Other amino acids needed no correction.

RESULTS

PROXIMATE ANALYSIS

The mean values of at least three determinations of each constituent are given in Table I.

TABLE I. Proximate analysis of bulk preparation of cod tropomyosin.

Constituent	Content	Constituent	Content
	%		%
Moisture	2.93	Nitrogen	15.44
Ash	3.49	Sulphur	0.728
Nucleic acid	1.50	Cysteine+	
Actin	3.7*	cystine	0.575
Tropomyosin	88.4*	Tryptophan	0.032

*Total protein by difference; the ratio actin: tropomyosin = 4 : 96 determined by planimetry of electrophoretic pattern.

TERMINAL AMINO ACIDS

With Sanger's fluorodinitrobenzene method, no N-terminal amino acids were found. The C-terminal acid, liberated by treatment with carboxypeptidase, was isoleucine. The rates at which different amino acids were released from tropomyosin (Table II) were used to estimate their sequence in the molecule; the first three occurred in the order: $-\text{thr}_{\frac{1}{2}}\text{-ser}_{\frac{1}{2}}\text{-ileu}_1$.

TABLE II. Release of amino acids from cod tropomyosin preparation upon treatment with carboxypeptidase.

Duration of enzyme treatment	Intensities of amino acid zones on paper chromatograms ^a						
	Ileu	Ser	Thr	Asp	Ala	Gly	Glu
<i>minutes</i>							
0	0	0	0	0	0	0	0
15	20	10	5	1	1	0	2
30	30	30	10	3	2	1	4
60	40	30	20	10	5	3	6
120	80	30	20	20	15	10	8
240	100	30	20	20	20	10	8

^aThe technique used did not permit the detection of methionine. The intensities and times at which the several amino acid zones attained maximum values are indicated in bold type.

AMINO ACID CONTENT

Three hydrolysates of cod tropomyosin were analysed by the Spackman *et al.* (1958) method; several replicates were run on each hydrolysate, so that at least seven, usually ten, and sometimes fifteen values were obtained for each amino acid. The nitrogen contents of the hydrolysates were used to express the results in terms of millimoles amino acid per 17.46 g of nitrogen, the latter being the amount of nitrogen equivalent with 100 g of pure tropomyosin in the bulk preparation (calculated from Table I). This total nitrogen content was composed of nucleic acid-N 0.27 g, actin-N 0.69 g, tropomyosin-N 16.50 g (assuming identical nitrogen contents for actin and tropomyosin and 16.0% for nucleic acid). The mean amino acid contents, their standard errors, and the number of observations from which they were obtained are listed in Table III.

TABLE III. Amino acid content of bulk preparation of cod tropomyosin.

Amino acid	Number of analyses	Amount per 17.46 g N		Std. error Mean
		Mean	Std. error	
		<i>millimoles</i>	<i>millimoles</i>	<i>%</i>
Lysine	15	119.6	0.78	0.65
Histidine	15	6.98	0.07	1.00
Ammonia	15	66.9	1.34	2.00
Arginine	14	43.7	0.44	1.01
Aspartic acid	10	110.0	1.48	1.35
Threonine*	10	30.9	0.47	1.53
Serine*	10	36.6	0.41	1.13
Glutamic acid	10	212.5	1.98	0.93
Proline	7	3.14	0.10	3.18
Glycine	10	20.4	0.26	1.27
Alanine	10	105.1	1.27	1.21
Cystine/2	—	5.41†	—	—
Valine*	10	28.3	0.42	1.49
Methionine	10	20.3	0.23	1.13
Isoleucine*	10	31.8	0.31	0.97
Leucine	10	102.4	0.86	0.84
Tyrosine	10	16.7	0.19	1.14
Phenylalanine	10	4.89	0.12	2.45

*Corrected for hydrolytic losses.

†From S content less methionine-S (5.40) and from direct cystine determination (5.41).

DISCUSSION

The nitrogen content of pure cod tropomyosin, calculated from the nitrogen distribution in the bulk preparation, was 16.50%. This is slightly lower than the value of 16.7% usually accepted for other vertebrate tropomyosins (e.g. Bailey, 1948; Kominz *et al.*, 1954). However, direct determination of the nitrogen content of the highly purified cod tropomyosin preparation never yielded results

higher than 16.5%. The latter value has therefore been used in this paper as the actual value for cod tropomyosin.

The precision of all the amino acid values listed in Table III appears quite acceptable. Even the proline content, which is the least precise of the data because its value is low and the method is relatively insensitive for this amino acid, has a small standard error. To obtain the amino acid composition of pure cod tropomyosin from the data of Table III, a correction must be applied to the value for each acid for the amount of that acid contributed by the actin impurity of the bulk preparation. These corrections were determined by carefully analysing a preparation of highly purified cod actin³; the mean values of two determinations (unpublished results very similar to those of Kominz *et al.*, 1954) were used. The results are given in Table IV.

TABLE IV. Amino acid composition of cod tropomyosin.

Amino acid	Amount in bulk preparation (17.46 g N)	Amount in actin (0.69 g N)	Pure cod tropomyosin (16.50 g N)	Recovery of nitrogen in cod tropomyosin	
	millimoles	millimoles	millimoles	grams	%
Lysine	119.6	1.9	117.7	3.30	20.0
Histidine	6.98	0.72	6.26	0.26	1.6
Ammonia	66.9	4.5	62.4	0.87	5.3
Arginine	43.7	1.6	42.1	2.36	14.3
Aspartic acid	110.0	3.2	106.8	1.50	9.1
Threonine	30.9	2.4	28.5	0.40	2.4
Serine	36.6	2.0	34.6	0.48	2.9
Glutamic acid	212.5	4.0	208.5	2.92	17.7
Proline	3.14	1.69	1.45*	0.02	0.1
Glycine	20.4	3.0	17.4	0.24	1.5
Alanine	105.1	2.8	102.3	1.43	8.7
Cystine/2	5.41	0.20	5.21	0.07	0.4
Valine	28.3	1.9	26.4	0.37	2.2
Methionine	20.3	1.3	19.0	0.27	1.6
Isoleucine	31.8	2.4	29.4	0.41	2.5
Leucine	102.4	2.6	99.8	1.40	8.5
Tyrosine	16.7	1.4	15.3	0.21	1.3
Phenylalanine	4.89	1.06	3.83	0.05	0.3
			Totals	16.56	100.4

*Proline by direct determination on highly purified tropomyosin: 1.88.

As may be seen, the corrections were usually small compared with the uncorrected values. This was not so for proline. To check the result for that amino acid, direct determinations were made on the highly purified preparation of cod tropomyosin; the value obtained was 1.88 millimoles per 16.50 g of nitrogen, considerably higher than the value of Table IV, and probably more accurate.

A comparison of the amino acid content found for cod tropomyosin with the values reported elsewhere for various other tropomyosins (Table V) shows

clearly the similarity between cod tropomyosin and other vertebrate tropomyosins. It is also evident, however, that there are many differences. The most striking among the latter is that in aspartic acid content. In this respect, cod tropomyosin appears to resemble invertebrate tropomyosin more than the vertebrate type. This difference could not be explained on the basis of lack in precision of some of the listed values, an explanation which might be used for smaller differences in some of the other amino acid contents. The possibility still remains that differences in purity of the various preparations might account for the dissimilarity of the aspartic acid values.

If the general similarity between cod tropomyosin and other vertebrate tropomyosins may be interpreted to indicate that the molecular weight of its monomer must be of the order of 53,000, as it was found to be for the rabbit muscle protein (Adair *et al.*, 1949; Tsao *et al.*, 1951; Tsao and Bailey, 1953), the number of amino acid residues and the molecular weight could be calculated from the amino acid composition. This has been done in Table VI.

TABLE VI. Amino acid residues per molecule of cod tropomyosin.

Amino acid	Minimal molecular weight from amino acid composition	Number of residues for MW = app. 53,000	Molecular weight from number of residues
Lysine	850	62	52,700
Histidine	16,000	3	48,000
Amide	1,600	33	52,800
Arginine	2,400	22	52,800
Aspartic acid	940	56	52,600
Threonine	3,500	15	52,500
Serine	2,900	18	52,200
Glutamic acid	480	110	52,800
Proline	53,200	1	53,200
Glycine	5,700	9	51,300
Alanine	980	54	52,900
Cystine/2	19,200	3	57,600
Valine	3,800	14	53,200
Methionine	5,300	10	53,000
Isoleucine	3,400	15	51,000
Leucine	1,000	53	53,000
Tyrosine	6,500	8	52,000
Phenylalanine	26,100	2	52,200
Total:		488	Mean: 52,540
Less amide:		33	
Residues per molecule:		455	

In earlier investigations, tropomyosin was considered not to contain proline. More recently, however, positive proline contents have been found (see Table V). It is evident from the results of this study that proline is definitely a constituent of cod tropomyosin and that there is probably one residue per molecule of the protein.

The occurrence of three residues of half-cystine (cystine/2) is of interest. This same number of residues was found by Saad *et al.* (1959) for carp tropomyosin but one less was reported by Kominz *et al.* (1954) for several other vertebrate tropomyosins. At least one of the half-cystine residues must be present in the cysteine form; the others may be present as two cysteines or as one cystine residue forming an -S-S- bridge in the molecule. The latter appears more likely when considering that oxidation of tropomyosin with performic acid prior to digestion with trypsin eliminated the initial lag-phase which was found when the digestion was carried out without previous oxidation (to be published). The presence of one -S-S- cross-linkage in the tropomyosin molecule is in agreement with the findings of Szent-Györgyi *et al.* (1959) for tropomyosin from rabbit muscle.

The absence of a free N-terminal residue and the occurrence of isoleucine in the C-terminal position agrees with findings for other tropomyosins (Bailey, 1951; Locker, 1954; Saad *et al.*, 1959). The C-terminal sequence in cod tropomyosin is exactly the same for the first three residues as that reported by Locker (1954) for rabbit tropomyosin. Beyond the third residue, the digestion results (see Table II) appear to indicate some differences. The most likely sequence based on the results of Table II is: -glu-gly-ala-as₂p-ileu-thr-ser-ileu. However, the reliability of this result decreases with increasing distance from the C-terminal residue, and judgement must be reserved until more accurate results become available.

ACKNOWLEDGMENT

The authors take pleasure in acknowledging the continuous interest and cooperation of Dr J. R. Dingle and Dr P. H. Odense throughout this investigation.

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Observations on the Ecology of the Pacific Cod (*Gadus macrocephalus*) in Canadian Waters^{1, 2}

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ABSTRACT

In Canadian waters, Pacific cod are close to the southern limit of their range and appear to inhabit depths where temperatures are between 6° and 9°C. Seasonal variations in depth distribution are not as pronounced as those in the northwestern Pacific where there are much greater variations in the seasonal cycle of temperature.

Relatively high temperature experience in Canadian waters appears to be responsible for a more rapid initial growth rate (instantaneous rate, $g = 1.99$ between ages I and II; 0.64 between ages II and III, decreasing to 0.19 between ages IV and V) and a much shorter life span than elsewhere. Estimates of L_{∞} , the asymptotic length, range from 72.8 cm to 77.4 cm, while estimates of K , the rate at which growth approaches L_{∞} , range from 0.56 to 0.71.

Maturity is reached at two to three years of age—several years earlier than in colder regions of the North Pacific—and estimates of instantaneous total mortality rate range from 1.27 to 1.77 for fish of commercial size. Although these are probably overestimates, it is nevertheless apparent that total mortality rate is very high and that a large share is due to natural causes. Instantaneous natural mortality rate possibly exceeds 0.9.

INTRODUCTION

NOT WITHOUT GOOD REASON one is usually inclined to associate the word *cod* with the North Atlantic Ocean, for most of the world catch of gadoid fishes and particularly of representatives of the genus *Gadus* originates from that region. Less well known is the fact that cod of the genus *Gadus* contribute also to the fisheries production of the North Pacific Ocean, though admittedly in much smaller measure. The Pacific cod (*Gadus macrocephalus*), or grey cod as it is called by Canadian fishermen, is widely distributed, but its potential importance, at least along the shores of North America, is still a matter for conjecture. In the past decade the cod has risen to considerable prominence in the trawl fishery off the Canadian coast and consequently has created a need for knowledge of its ecology and population dynamics.

Extensive published data exist on the biology and ecological relationships of cod in waters of the northwestern Pacific, but only fragmentary information is available for the northeastern region.

This paper summarizes results of recent studies conducted by the Fisheries Research Board on the ecology of the cod in Canadian waters. Preliminary

¹Received for publication February 23, 1961.

²Parts of this paper were presented at a Symposium on Fisheries Oceanography held at San Diego, California in June, 1959. Other contributions to the symposium are to be published in a report of the California Co-operative Oceanic Fishery Investigations.

and approximate though some of the observations may be, an attempt has been made to draw comparisons with results of USSR investigations in the north-western Pacific, a region which is ecologically quite different from the north-eastern Pacific.

Along the Canadian coast, the Pacific cod is close to the southern limit of its range. Data to be presented suggest that in this region environmental stress, imposed either directly or indirectly by relatively high water temperature, is manifest in a high initial growth rate, early sexual maturity and a short life span.

NOMENCLATURE AND DISTRIBUTION OF THE PACIFIC COD

In North American literature the Pacific (grey) cod is recognized as *Gadus macrocephalus* Tilesius. It is similar in many respects to the famous Atlantic cod, *G. morhua* L., but on the basis of certain anatomical features (shape of the air bladder horns, colour of peritoneum and fins, etc.) Schultz and Welander (1935: 130) concluded that it bears closer resemblance to the Greenland cod, *G. ogac* Richardson. Some research workers in the USSR (but not all—cf. Rass, 1959: 244) regard these three species as subspecies of *G. morhua*, whence the Pacific cod becomes *G. morhua macrocephalus* (Svetovidov, 1948: 179; Moiseev, 1960: 558). In any event it is generally accepted that there is but one representative of the genus *Gadus* in the North Pacific Ocean and adjoining seas, and in this paper it will be referred to as *G. macrocephalus*, even though it may be deserving of only sub-specific rank.

Gadus macrocephalus is widely distributed around the great arc of the North Pacific Ocean (Fig. 1). Along the shores of eastern Asia, the southern limit of its range (not shown in the figure) is reported to be in the Yellow Sea along the west coast of Korea. Progressing northward, the Pacific cod is found along the eastern and western shores of the Sea of Japan, around the shores of Hokkaido and Sakhalin and along the Kurile Island chain. It occurs in the Sea of Okhotsk, along the east coast of Kamchatka and in the western Bering Sea as far north as the Gulf of Lavrentsia (Svetovidov, 1948: 180).

Along the coast of western North America, the northern limit of the cod's range is reported to be in the latitude of St. Lawrence Island (and around that Island, according to Cobb, 1927: 388). It occurs in the southeastern Bering Sea and apparently also along the Aleutian Island chain. To eastward, the cod is found along the Pacific side of the Alaska Peninsula, around the shores of the Gulf of Alaska and from there southward to the California coast of the United States.

The region between Cape Flattery and Destruction Island on the Washington coast (48°21' N to 47°40' N Lat.) may be regarded as the southern limit of fishing specifically for cod. Southward from Destruction Island, catches of cod are usually incidental to those of other species, and cease to be recorded in fishery statistics for waters south of Cape Blanco, Oregon (42°50' N Lat.). Occasionally,

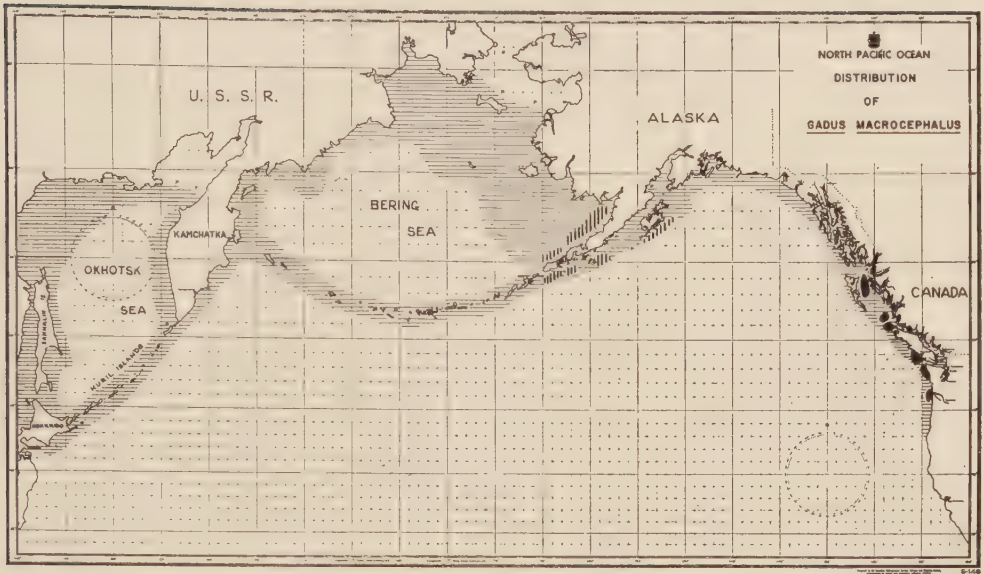


FIG. 1. General distribution of *Gadus macrocephalus* in the North Pacific Ocean and adjoining seas, adapted from Svetovidov (1948). Vertical shading depicts approximate location of the former fishery by North American nationals near the Alaska Peninsula, while solid areas refer to the present day fishery off Canada and the northwestern United States.

individual specimens are reported from California waters as far south as Pt. Piedras Blancas ($35^{\circ}33'$ N Lat.—see Phillips, 1950: 439; 1951: 351; 1953: 559; 1958: 349).

PRODUCTION OF PACIFIC COD

1. GENERAL

The reported production of Pacific cod in 1957, according to fishery statistics published by the Food and Agriculture Organization of the United Nations, was 94,500 metric tons (about 200 million pounds) or less than one-twentieth of the cod production from the North Atlantic Ocean and adjoining seas. Of this catch, 69.5% was accounted for by Japan, 19.5% by the USSR, 5.7% by the USA, 3.2% by Canada and 2.1% by South Korea (no information was available on production by North Korea).

2. NORTH AMERICAN WATERS

The fishery by North Americans for Pacific cod has a long and varied history, beginning in the early 1860's with landings at San Francisco from the Sea of Okhotsk (Cobb, 1927: 404). This long-distance operation continued in prominence until 1884, after which time grounds closer to home, principally those in the southeastern Bering Sea and along the southern shores of the Alaska Peninsula, assumed a dominant role. This latter fishery, pursued with hook and line, reached a peak production of 3,893,000 fish or roughly 44,000,000 lb (round

TABLE 1. Production of Pacific cod from waters adjacent to Canada and the States of Washington and Oregon, in millions of pounds estimated round weight. Sources: British Columbia catch statistics, Department of Fisheries, Canada; records of the Fisheries Research Board of Canada; Fishery Statistics compiled by the Pacific Marine Fisheries Commission.

Year	Canada	Washington	Oregon	Total
1935	2.24	0.05	—	2.29
36	1.08	0.26	*	1.34
37	1.92	0.53	0.01	2.46
38	2.50	0.46	—	2.96
39	2.23	0.66	—	2.89
1940	2.23	0.65	—	2.88
41	1.29	1.57	*	2.86
42	0.90	1.18	0.03	2.11
43	2.12	1.03	0.03	3.18
44	1.26	1.04	0.03	2.33
1945	1.60	4.08	0.07	5.75
46	2.86	4.36	0.25	7.47
47	0.94	2.45	0.03	3.42
48	0.92	5.38	0.03	6.33
49	1.68	5.50	*	7.18
1950	2.47	6.35	0.04	8.86
51	5.72	8.42	0.12	14.26
52	4.89	10.00	0.12	15.01
53	3.45	8.20	0.18	11.83
54	5.70	15.41	0.78	21.89
1955	4.62	12.61	0.32	17.65
56	5.15	9.57	0.18	14.90
57	8.50	11.32	0.69	20.51
58	10.02	12.29	0.30	22.61
59	9.19	12.91	0.30	22.40

*Less than 5000 lbs.

weight) in 1916³. However, mainly because of economic problems, it declined to a relatively low level by 1933, where it remained until the late 1940's before proceeding to virtual extinction in the past decade.

The only other area along the North American coast where Pacific cod have been the object of extensive fishing is that adjacent to Canada and the State of Washington. In contrast to the history of events in western Alaska, this southern fishery is of relatively recent origin and is still in process of development.

Rapid development of an otter-trawl fishery for many species of groundfish along the exposed coast of British Columbia resulted in a substantial increase in cod production in the years following World War II (Table 1). Between 1945

³These figures apply to the catch secured by the shore and vessel fisheries and transported to ports in Washington and California. Cod used for local consumption in Alaska are not included. Conversion to round weight is based on Cobb's data (1927: 444) for the years 1922 to 1925.

and 1950 the annual catch by Canadian and United States trawlers averaged about 6,500,000 lb, after which time it rose to new heights, principally in response to the demand for "fish sticks". Since 1951 the catch has varied between 12,000,000 and 23,000,000 lb per year with an average of 18,000,000 lb for the years 1951 to 1959.

DISTRIBUTION OF COD IN WATERS ADJACENT TO CANADA

1. AREAS OF CONCENTRATION

While the Pacific cod occurs throughout Canadian coastal waters generally, it forms concentrations in well-defined areas and at particular times of the year. Fisheries involving Canadian and United States trawlers take place on these concentrations and are confined to relatively small segments of the continental shelf (Fig. 2). The most productive fishing areas lie in northern Hecate Strait including four main fishing grounds: "White Rocks" or Banks Island; the Warrior-Butterworth "edge" which is confluent with the "Two Peaks" ground at the northern end of the Strait and the Horseshoe-Cumshewa grounds in the lower central area. Farther to the south, in Queen Charlotte Sound, Pacific cod are taken principally along the southeastern edge of Goose Island Bank and along the northern edge of Cape Scott Bank. Off the lower west coast of Vancouver Island, cod are encountered on a number of restricted grounds (known locally as the "Firing Range", "Cabbage Patch" and "Forty-mile" or Big Bank) within the general confines of La Pérouse Bank, and also on or near Swiftsure Bank at the entrance to Juan de Fuca Strait. Still farther to the south, off the coast of the United States, concentrations are found mainly between Cape Flattery and Destruction Island, Washington. Minor quantities are encountered off the estuary of the Columbia River and the coast of Oregon. In addition to the offshore fishing areas, there are numerous small fishing grounds for cod within Canadian and United States territorial waters of the Strait of Georgia and Puget Sound.

2. SEASONAL BATHYMETRIC DISTRIBUTION

Information on seasonal changes in the depths occupied by Pacific cod on banks adjacent to British Columbia has been obtained through a system of interviewing Canadian trawler captains. At time of landing, a report is obtained on the area of catch, hours of fishing, the catch of each species and the depths at which they were caught. While the reported depth of fishing is usually indicated by a range of depths, for particular fishing grounds it is usually narrow enough to permit calculation of a meaningful average depth. Reports of various fishermen are combined (with due weight given to size of catch) in order to obtain an average picture for each month and area. The data, as presented here, have been further consolidated to provide an average of conditions observed during the period 1954-58, inclusive. Throughout, only those individual landing records have been used in which at least 25% of the fare consisted of cod. This

arbitrary selection reduces, but does not entirely eliminate, the effect of concurrent fishing for species other than cod.

For none of the fishing grounds is it possible to trace the bathymetric cycle throughout the year, strictly from observation of the Canadian fishery. Fishing on offshore banks is limited seasonally by weather and also by seasonal variations in the availability of cod. It is possible, nevertheless, to infer, from trends in depth distribution evident during seasons of active exploitation, what the probable course of events is at other times of the year. Support for these inferences is to be found in information on the fishing pattern of the United States fleet, which is able to operate in exposed waters more or less on a year-round basis.

In general, the seasonal pattern of fishing suggests that cod inhabiting waters along the Canadian coast engage in a seasonal bathymetric cycle of migration. Greatest depths are reached in the winter months. Following spawning (January to March, depending on area) a migration takes place towards shallower regions of the coastal banks and this continues until late spring or early summer. The return movement to deeper water begins in mid-summer and continues until November or December. The vertical range of depths occupied during the year varies from area to area, but, as will be shown later, it is considerably less than that observed in most regions adjacent to the coast of Asia.

(a) HECATE STRAIT

During the months of November through February, Canadian trawlers are attracted to the White Rocks (Banks Island) ground which appears to be the principal spawning area for cod in Hecate Strait. At that time of year they are taken mainly between depths of 55 to 65 fathoms (100–120 m). Spawning apparently reaches a peak during the month of February, after which catch per unit of effort begins to decline. Coincident with this decline a fishery for cod begins to develop 30 to 60 miles to the northward along the Butterworth-Warrior edge and on the Two Peaks ground. Fishing in this region usually reaches its maximum in April, at which time the average depth inhabited by the cod is approximately 40 fathoms (about 75 m).

A northward migration from the White Rocks ground to shallow grounds in the northern part of the Strait is suggested by this northward movement of the fishery, but remains to be substantiated by tagging⁴. If true, it would accord with observations on the seasonal migrations of the lemon sole or English sole (*Parophrys vetulus*) in the same general area (cf. Ketchen, 1956: 659).

Usually from late April through early June, cod are encountered at depths of 30 to 35 fathoms (55–65 m) and in some years may be found right on the

⁴At time of writing it is too early to comment fully on the results of tagging conducted during February, 1960, on the White Rocks grounds. Initial recaptures were mainly from the area of tagging with 17 from the Two Peaks ground (60 miles to the north of the tagging site). However, there were also 4 returns from the Horseshoe ground (45 miles south of the tagging site).

edge of the bank as shallow as 17 to 20 fathoms (31–37 m). In northern Hecate Strait, the cod fishery usually comes to an end in late spring, because the cod either cease to remain in sufficient concentration to attract fishing or move into areas which cannot be touched with trawl nets.

About 80 miles to the south of the Butterworth-Warrior "edge", namely, on the Horseshoe ground, a fishery for cod usually develops in late spring and, as on the northern grounds, it occurs in relatively shallow water between 26 and 40 fathoms (48–73 m). These fish may be emigrants from the winter spawning area at White Rocks or they may belong to a separate population having its wintering ground in southern Hecate Strait.

From June onwards cod become increasingly scarce on all fishing grounds in Hecate Strait. Available records suggest that the months of May to June mark the period of maximum advance towards shallow water and that thereafter they move gradually towards deep water where they once again become available to the fishery (usually in November).

The foregoing remarks are best summarized by the data in Table II which provides a composite picture (weighted to the relative size of the catch on the various grounds) of the bathymetric distribution of cod in Hecate Strait. As a rule, greatest depth are reached in November (average 66 fathoms or 120 m) and shallowest depths in May or June (34–35 fathoms or 62–64 m).

TABLE II. Monthly average depth distribution of cod in Hecate Strait as based on observations for years 1954–55 to 1957–58, inclusive. (1 fathom = 1.83 m).

In this and succeeding tables, data based on fewer than 10 observations are in brackets.

Month	Number of observations	Depth (<i>fathoms</i>)		Month	Number of observations	Depth (<i>fathoms</i>)	
		Av.	Range			Av.	Range
Oct.	(2)	(38)	(30–41)	Apr.	71	14	39–42
Nov.	17	66	52–75	May	64	34	22–41
Dec.	19	58	54–64	June	22	35	18–47
Jan.	42	55	48–69	July	15	43	41–45
Feb.	45	56	53–65	Aug.	(2)	(44)	(42–45)
Mar.	119	49	45–55	Sept.	(2)	(53)	(52–54)

(b) QUEEN CHARLOTTE SOUND

The principal fishing grounds for cod in this area lie along the southeastern edge of Goose Island Bank and the northern edge of Cape Scott Bank. Insofar as the Canadian fleet is concerned, the fishery occupies a fairly short period of each year, usually May to August. Thus, there exists only fragmentary information on the seasonal bathymetric cycle. As in Hecate Strait, there is a suggestion that shallowest depths are reached in the months of May and June: about 46 to 51 fathoms (84–93 m) on Cape Scott Bank; about 56 fathoms (102 m) on Goose Island Bank (see Tables III and IV). Thereafter a movement towards

TABLE III. Monthly average depth distribution of cod on Cape Scott Bank as based on observations for years 1954-55 to 1957-58 inclusive.

Month	Number of observations	Depth (<i>fathoms</i>)		Month	Number of observations	Depth (<i>fathoms</i>)	
		Av.	Range			Av.	Range
Oct.	(1)	(56)	(45-67)	Apr.	18	52	49-55
Nov.	(1)	(83)	(82-85)	May	36	46	43-52
Dec.	(2)	(35)	(30-52)	June	36	51	44-58
Jan.	(1)	(55)	—	July	26	62	55-71
Feb.	(0)	—	—	Aug.	26	63	59-67
Mar.	(9)	(44)	(43-45)	Sept.	(5)	(64)	(59-68)

TABLE IV. Monthly average distribution of cod on Goose Island Bank as based on observations for years 1954-55 to 1957-58 inclusive.

Month	Number of observations	Depth (<i>fathoms</i>)		Month	Number of observations	Depth (<i>fathoms</i>)	
		Av.	Range			Av.	Range
Oct.	(1)	(59)	—	Apr.	(5)	(58)	(55-61)
Nov.	0	—	—	May	19	57	57-58
Dec.	0	—	—	June	20	56	50-62
Jan.	0	—	—	July	21	61	60-63
Feb.	0	—	—	Aug.	(8)	(63)	—
Mar.	(1)	(72)	—	Sept.	(1)	(60)	—

deeper water is indicated, although there is a scarcity of reliable data for months beyond August.

These observations are in general accord with those of Alverson (1960), based on records of the United States trawl fishery for cod on the Cape Scott and Goose Island Banks. Alverson's data (1955-57 average) suggest that cod on the latter bank reached their shallowest depth, about 60 fathoms (110 m), between May and July and their greatest depth, about 75 fathoms (135 m), in mid-winter. On Cape Scott Bank, shallowest depths were reached between June and August (about 65 fathoms or 120 m) and greatest depths in early winter (about 78 fathoms or 143 m)⁵.

In comparison with Hecate Strait, the cod of Queen Charlotte Sound appear to occupy greater depths throughout the year and the amplitude of the annual bathymetric cycle is less.

⁵While Canadian observations are in general accord with those of United States investigators in respect to the timing and direction of seasonal changes in depth distribution, the observed absolute depths are somewhat less. Probably this can be attributed to the fact that Canadian and United States trawling fleets in Queen Charlotte Sound fish with different emphasis on species of groundfish which occur more or less in association with Pacific cod. In general the Canadian fleet fishes for shallow-water species such as rock sole (*Lepidopsetta bilineata*) as well as cod, while the United States fleet operates with greater emphasis on deep-water fishes (such as *Sebastes* spp.). This serves to emphasize the limitations of commercial catch records for making observations on a particular species when fishing interest is not restricted entirely to that species. Although an attempt has been made to select out the effects of fisheries for species other than cod it can be done with only partial success.

(c) LOWER WEST COAST OF VANCOUVER ISLAND

The most southerly of the important fishing areas for cod in Canadian waters are La Pérouse Bank and Swiftsure Bank. Because of the topography of the former, it is difficult for the fishing fleet to maintain contact with cod schools for any great length of time each year. The range of fishable depths on grounds frequented by cod is limited, and hence if they move away they cannot be followed as systematically as on the Cape Scott and Goose Island Banks. Thus the fishery is usually compressed to a very few months, and seasonal trends in depth are more difficult to detect.

On the so-called Firing Range (a small basin on the inshore side of La Pérouse Bank) cod are caught usually between depths of 35 and 43 fathoms (65–80 m) during the May-July period. At the same time of year the nearby "Cabbage Patch" yields its best catches and these originate from depths of 36 to 40 fathoms (66–73 m). On the southeast and southwest corners of La Pérouse, namely, on Forty-mile Bank (Big Bank), cod fishing comes into prominence in the late summer and fall, after production from inshore grounds has passed its peak. Here the depths of fishing range from 40 to 46 fathoms (73–84 m), somewhat deeper than on inshore banks.

Catches from the Swiftsure Bank area, at the entrance to Juan de Fuca Strait, are made principally in the May-July period and at depths of 24 to 28 fathoms (44–51 m).

Table V is a composite of observations on the various fishing grounds off the lower west coast of Vancouver Island. Cod appear to be most available to the Canadian fleet during the inshore or shallow-water phase of the annual bathymetric cycle. As in regions farther to the north, there appears to be a movement toward deeper water during the late summer and early fall. Again, these observations are in general agreement with those made by Alverson (1960) on the cod fishery by United States vessels on adjacent grounds, between Cape Flattery and Destruction Island. There, during 1955-57, shallowest depths appeared to be reached about July or August (35–45 fathoms or 76–78 m).

TABLE V. Monthly average depth distribution of cod on grounds off the lower west coast of Vancouver Island, as based on observations for years 1954–55 to 1957–58, inclusive.

Month	Number of observations	Depth (<i>fathoms</i>)		Month	Number of observations	Depth (<i>fathoms</i>)	
		Av.	Range			Av.	Range
Oct.	22	43	37–47	Apr.	35	35	24–52
Nov.	(8)	(43)	(40–48)	May	89	37	24–44
Dec.	0			June	73	35	24–46
Jan.	0			July	21	36	23–49
Feb.	0			Aug.	13	38	31–43
Mar.	(8)	(30)	(23–45)	Sept.	15	45	39–58

In the winter months the cod were usually encountered at depths between 60 and 65 fathoms (110–120 m).

SEASONAL MOVEMENTS IN RELATION TO THE PHYSICAL ENVIRONMENT

In the foregoing section, the seasonal bathymetric distribution of cod in waters adjacent to the Canadian coast was described in rather general terms. For particular years and areas it is possible to draw some approximate comparisons with observations of seasonal changes in the oceanography of the continental shelf—if only to gain a preliminary appreciation of the cod's environmental experience in this southern part of its range.

A series of synoptic oceanographic surveys in Hecate Strait and Queen Charlotte Sound was first undertaken by the Pacific Oceanographic Group between May 1954 and June 1955. Data from a few of the numerous stations occupied during these surveys have been selected for comparison with observations on the movements of cod. The positions, chosen for their proximity to known cod fishing grounds, are shown in Fig. 2, as Stations A, B and C, adjacent to the Two Peaks, White Rocks and Goose Island-Cape Scott grounds, respectively.

Synoptic surveys of the continental shelf were resumed in May of 1957, along the west coast of Vancouver Island and in the entrance to Queen Charlotte Sound. Oceanographic data for the years 1957 and 1958 are based on observations at Stations D and E, at the entrance to the Cape Scott-Goose Island gully and at the edge of La Pérouse Bank, respectively. In addition there are available, for these years, twice-daily bathythermograph observations from the lightship at Swiftsure Bank (Station F in Fig. 2). These observations together with those for the other stations mentioned are taken from the published data records of the Pacific Oceanographic Group.

The synoptic surveys of 1954–55 were made at 2-month intervals, while those of 1957–58 were made at 3- to 4-month intervals. Clearly, such infrequent monitoring cannot be expected to provide more than a broad description of the cod's physical environment. In the present study, primary consideration has been given to the relationship between temperature and the movement of cod. The main reason for this exclusive and undoubtedly oversimplified treatment is that it provides a convenient means of drawing comparisons with observations which have been made in the northwestern region of the Pacific. Nevertheless, there is a substantial weight of evidence in support of the view that temperature plays an important role in the general distribution, behaviour and metabolic processes of the cod. Hence, while acknowledging the possible influence of such factors as salinity, oxygen concentration, pH, etc. and the possibility that temperature may at times be of only indirect importance, we shall proceed to examine the relationship between the seasonal cycle of temperature and the seasonal bathymetric distribution of the cod, first in Canadian waters and then in the northwestern Pacific.



FIG. 2. Principal trawling grounds for Pacific cod on banks along the Canadian coast and positions of hydrographic Stations A-F referred to in the text.

1. OBSERVATIONS IN CANADIAN WATERS

(a) HECATE STRAIT AND QUEEN CHARLOTTE SOUND

Figures 3, 4 and 5 show the seasonal variations in temperature structure at Stations A, B and C, respectively, as derived from the 1954-55 surveys of the northern British Columbia coast. Shown also are the average depths and ranges of depths over which cod were encountered in economic concentrations by the Canadian trawler fleet.⁶

On the Two Peaks ground at the extreme northern end of the Hecate Strait Bank, data on cod distribution are rather fragmentary, as the fishery occupies a very short period of the year (Station A, Fig. 3). These limited observations, in a region which is representative of the coldest conditions on the British Columbia coast, suggest that during 1954 and 1955 cod occupied water of approximately 6° to 7°C.

During this same period on the main fishing grounds on Hecate Strait, namely, between the Butterworth-Warrior "edge" and the Horseshoe ground (Station B, Fig. 4) a majority of the records suggests that cod remained within the range of 6° to 8°C throughout the period of observation. Virtually all were within the range of 6° to 9°C.

Farther to the south in Queen Charlotte Sound (Station C, Fig. 5) commercial catches of cod were obtained by Canadian trawlers at depths where water temperature was between 6° and 7°C. For the early months of 1955, information on depth distribution is available in data from the United States fishery. Average depths for the months of January through March, 1955, shown in Fig. 5 are from Alverson (1960: 56-57). Temperature at these depths was roughly 6° to 7°C.

Thus, it appears that cod in the northern part of the Canadian coast inhabited waters of 6° to 7°C, more or less throughout the year.

From May, 1957, onwards, oceanographic surveys of coastal and high seas regions have provided a certain amount of information on the seasonal cycle of temperature at Station D (see Fig. 2). This Station lies westward of Station C, in the entrance to the trench which separates the Goose Island and Cape Scott Banks. As shown in Fig. 6, the 1957 and 1958 distribution of Canadian cod catches (with the exception of those on the Cape Scott Bank in 1958) was largely within the range of 6° to 7°C. All were within the 6° to 9°C range. Figure 6 includes data from the United States fishery in October, November and December, 1957 (from Alverson, loc. cit.). In those months, cod appeared to be occupying depths where temperatures were between 7° and 8°C.

Reviewing the results for northern British Columbia waters, it appears that cod are to be found most commonly at depths where temperatures are between 6° and 7°C. Almost all of the commercial catches are made within the 6° to 9°C range.

⁶Because temperature is plotted on a time-depth scale, the impression is created in these figures that cod are caught in mid-water. Actually they are caught on or near the bottom.

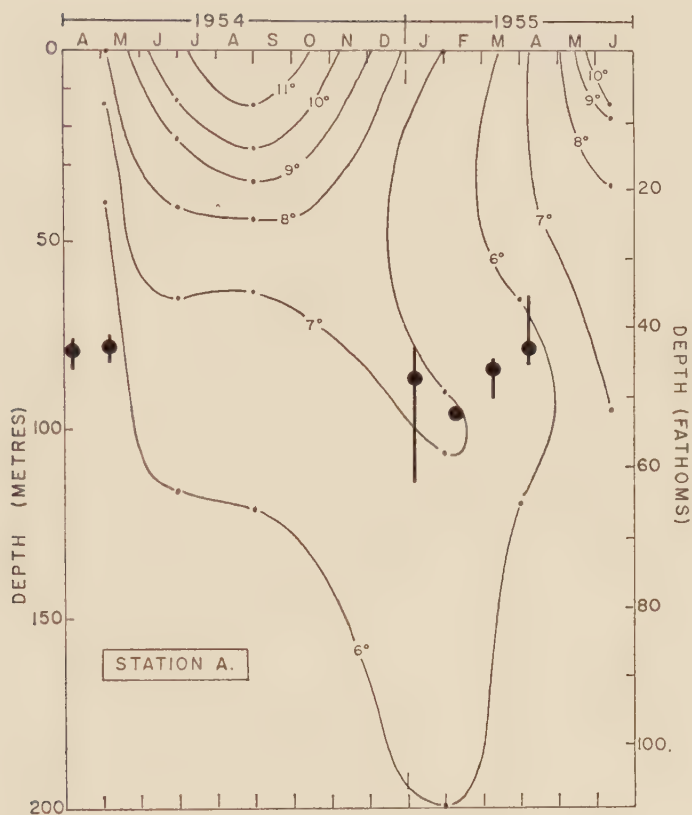


FIG. 3. The seasonal cycle of water temperature at Station A and its relation to the monthly depth distribution of Canadian commercial catches of cod from the Two Peaks ground in northern Hecate Strait during 1954-55.

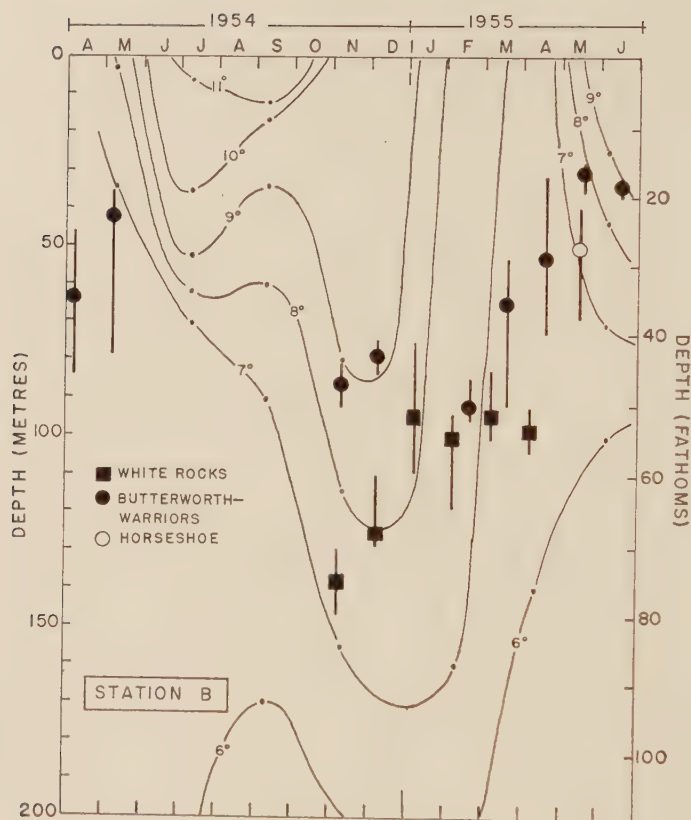


FIG. 4. The seasonal cycle of water temperature at Station B and its relation to the monthly depth distribution of Canadian commercial catches of cod from the Butterworth-Warrior, White Rocks and Horseshoe grounds of Hecate Strait during 1954-55.

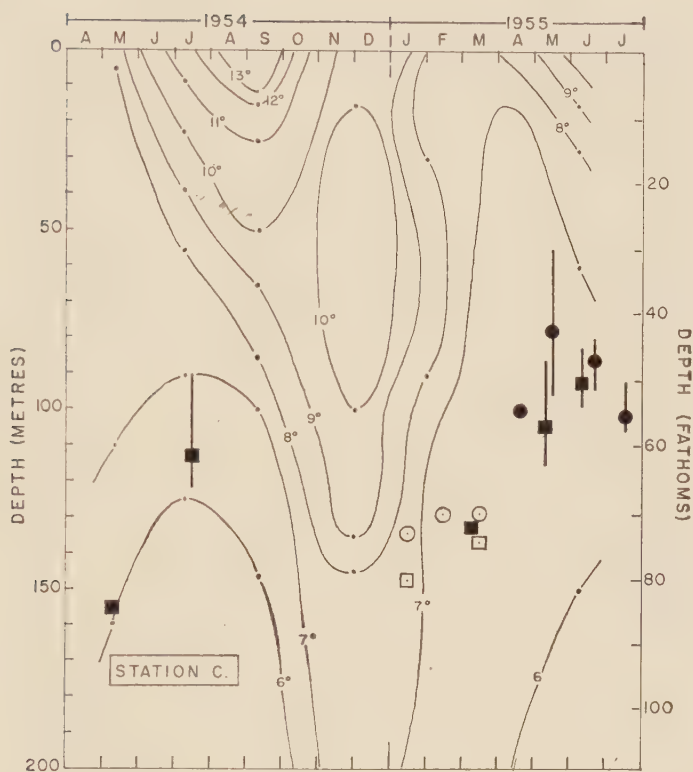


FIG. 5. The seasonal cycle of water temperature at Station C and its relation to the monthly depth distribution of Canadian commercial catches of cod on the Goose Island ground (solid squares) and Cape Scott ground (solid circles) in Queen Charlotte Sound during 1954-55. Data pertaining to the United States fishery in these areas during January-March, 1955, shown as open squares and open circles, respectively.

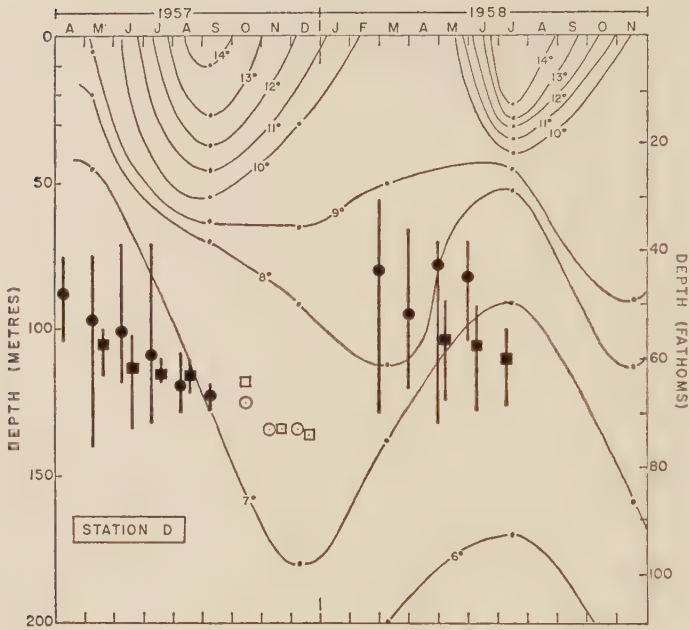


FIG. 6. The seasonal cycle of water temperature at Station D and its relation to the monthly depth distribution of Canadian commercial catches of cod on the Goose Island ground (solid squares) and Cape Scott ground (solid circles) in Queen Charlotte Sound during 1957-58. Data pertaining to the United States fishery in these areas during October-December, 1957, shown as open squares and open circles, respectively.

(b) LOWER WEST COAST OF VANCOUVER ISLAND

Synoptic oceanographic data for this southern region of the Canadian coast are based on observations at Station F (Fig. 2). These are presented in Fig. 7 with related information on cod distribution for the period 1957-58. Most of the latter data fall between the isotherms of 7° and 8°C, but in a few cases, it is suggested that catches were made at temperatures up to 10°C.

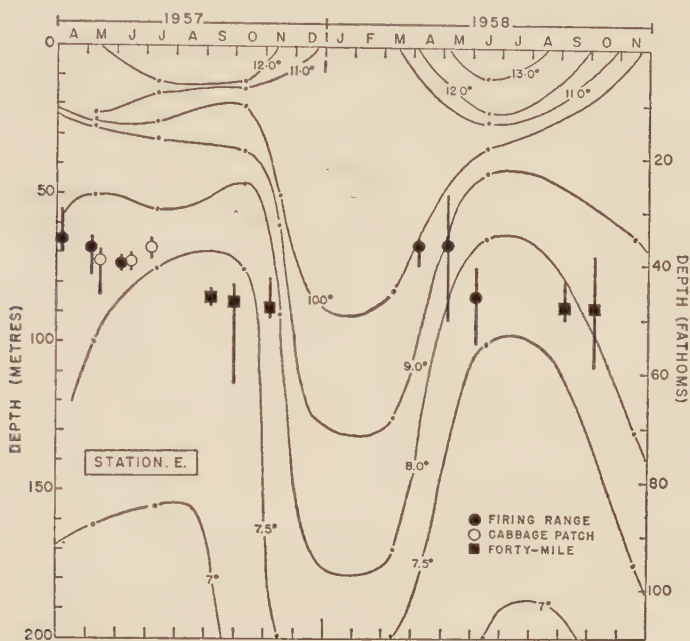


FIG. 7. The seasonal cycle of water temperature at Station E and its relation to the monthly depth distribution of Canadian commercial catches of cod on various grounds associated with La Pérouse Bank, off the lower west coast of Vancouver Island in 1957-58.

Average depths of fishing by United States trawlers during October, November and December, 1957, on the adjacent Cape Flattery-Destruction Island grounds were 51, 66 and 57 fathoms, respectively (data from Alverson, 1960: 56). Station E temperature for these months and depths were roughly within the range of 7.5° to 9.5°C.

These observations for the general area of La Pérouse Bank suggest that cod inhabit slightly warmer water than in regions farther to the north (Queen Charlotte Sound and Hecate Strait). Observations at Swiftsure Bank (Station F in Fig. 2) seem to confirm the observations at Station E that cod do indeed inhabit water which is warmer than 8°C. A Canadian fishery occurs along the inshore side of Swiftsure Bank (about 6 miles NE of the lightship, 48°33'N, 124°49'W), mainly during the months of May to July. Cod are taken at depths

ranging narrowly between 22 and 26 fathoms (40–48 m). Monthly averages of twice-daily temperature readings at depths of 25 to 27 fathoms (as determined from the lightship bathythermograph data) are given in Table VI. Shown also are the May–July catches of cod from the Swiftsure area. Unfortunately, records of the fishing operations were not sufficiently voluminous or detailed to permit a breakdown of catch by day for comparison with the daily temperature observations. However Table VI suggests that cod were caught at temperatures at least as high as 7.7°C and probably as high as 9.0°C.

TABLE VI. Summary of temperature observations at Swiftsure lightship and record of Canadian cod catch on the Swiftsure Bank.

Year	Month	Temperature at 25 fathoms		Canadian catch
		Monthly mean	Range	
		°C	°C	lb
1957	May	8.5	7.9–8.9	79,000
	June	8.5	8.0–9.2	52,000
	July	8.5	8.0–8.7	20,000
1958	May	8.5	7.7–9.4	53,000
	June	8.9	8.2–9.5	59,000
	July	8.3	7.7–8.8	—

(c) STRAIT OF GEORGIA

In passing, it is worthwhile to comment on observations of cod distribution in the inshore waters of the Canadian coast. The main fishing grounds are in the Strait of Georgia, in particular localities along the east coast of Vancouver Island. One is Nanoose Bay, which is fished only during the months of February and March when cod are congregated there for spawning, at depths of 40 to 50 fathoms (70–90 m). Temperatures at these depths in March of 1950 appeared to be within the range of 7.5° to 8.5°C (cf. Waldichuk, 1957: 348).

(d) SUMMARY

On the basis of observations in 1954–55 and 1957–58, it appears that the main concentrations of Pacific cod on banks adjacent to the Canadian coast are to be found between the isotherms of 6° and 9°C. In the northern sector of the coast, they tend to favour the lower part of this range (6°–7°C) and the upper part (7°–9°C) in the southern sector. In some instances, noted only in the latter region, there may be occasions when cod occur in water which is over 9°C.

Although data are incomplete, there is evidence of a seasonal cycle in the depth distribution of cod which is more or less synchronous with the seasonal cycle of temperature. Greatest depths are reached by the cod during the November–February period (50 to 80 fathoms, depending on the area) and shallowest depths are reached during late spring or early summer (17–40 fathoms). Similarly, it is noted that the isotherms of 6°, 7° and 8° are generally deepest during winter and shallowest during late spring and early summer.

In the light of existing information it is, of course, impossible to say whether there is a direct, causal connection between changes in bottom temperatures and the inshore-offshore movements of cod. Such features as salinity and dissolved oxygen have been examined, but these fail to reveal variations which are synchronous with the movements of cod. However, the evidence in favour of water temperature must remain circumstantial until results of more detailed and direct studies are available.

2. OBSERVATIONS IN THE NORTHWESTERN PACIFIC OCEAN AND WESTERN BERING SEA

The Pacific cod has been under investigation for many years in waters adjacent to the Soviet Union, Japan and Korea. Results of numerous studies are conveniently summarized in a publication by Moiseev (1953).

Two opposing patterns of seasonal vertical migration are evident in the northwestern Pacific. In what Moiseev terms the north boreal region (from the northwestern reaches of Bering Sea to the latitude of the North Kurile Islands and Strait of Tartary) cod occur in deep water in the winter months and in shallow water during the spring and summer. Spawning occurs in late winter or early spring. In these respects the behaviour is rather similar to that observed in Canadian waters⁷. There is, however, a pronounced difference in the amplitude of the seasonal bathymetric cycle. During summer months, depths occupied are generally less than 30 fathoms (less than 50 m) and are even in the littoral zone in some regions. Wintering depths range from 135 to 150 fathoms (270-300 m) in the eastern part of the Sea of Okhotsk (west Kamchatka), from 82 to 110 fathoms (150-200 m) off southeastern Kamchatka, and from 90 to 135 fathoms (170-250 m) in the northwestern Bering Sea.

In the south boreal region of the western Pacific (south Kurile Islands to the western shores of Korea) the seasonal migration pattern is the reverse of that in the north boreal region. There, the cod inhabit relatively shallow water during winter months (15-50 m, 8-27 fathoms). Spawning occurs from December to February, depending on locality. With approach of summer the cod move to relatively deep water (100-250 m, 55-135 fathoms).

In the region from southwestern Sakhalin to Peter the Great Bay, where there is a transition between biogeographic features of the north and south boreal regions, behaviour of the cod is intermediate between that observed to north and south.

Typical differences in the seasonal cycle of depth distribution in Pacific cod of Asia and Canada are illustrated diagrammatically in Fig. 8, with no pretence to being representative of all situations within the broad area under consideration. In Canadian waters, (1) the annual range of vertical migration is about one-third of that in the western regions of the Pacific and (2) the timing of the migration

⁷According to the biogeographic classification presented by Rass (1959: 249) waters off the west coast of Canada lie on the boundary of the north and south boreal regions of the Pacific Ocean.

appears to correspond more or less with that in the northwestern (north boreal) region.

Note in Fig. 8 that Canadian waters have been classed as north boreal. In his classification of biogeographic regions of the Pacific Ocean, Rass (1959) separates the north and south boreal regions of the northeastern Pacific near Cape Scott (northern end of Vancouver Island). More detailed study of general zoogeography in this area may show that the boundary should be somewhat farther to the south. In any event, it is probable that Canadian waters should be classed as a transition zone between the two major divisions.

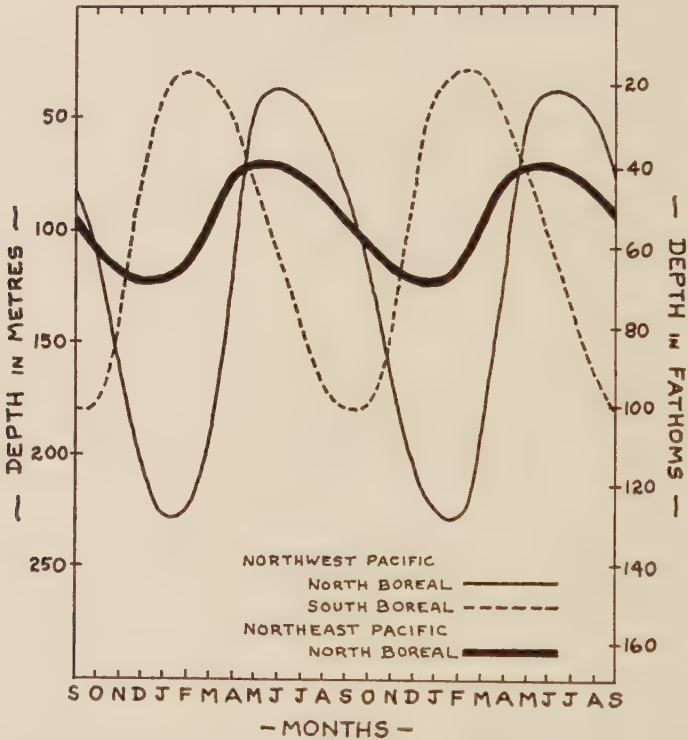


FIG. 8. Diagrammatic representation of the seasonal vertical migrations of cod in various regions of the North Pacific Ocean.

Moiseev (1953: 97) estimates that cod of the Pacific Ocean occur, broadly speaking, within the temperature range of -1.5° to $+18^{\circ}\text{C}$. However, by eliminating situations where conditions for growth, reproduction and survival are marginal, this range can be narrowed substantially. A range of 0° to 10°C would more aptly describe the conditions under which cod flourish in appreciable numbers.

In the north boreal region of the western Pacific, cod tend to avoid areas where temperatures fall below 0°C or rise above 10°C . During the summer

months, they are to be found generally between 2° and 6°C . In the western Bering Sea, "optimum" temperatures are between 0.2° and 4.5°C during summer (Moiseev's table 66). Temperatures at time of spawning (late winter) are between 0° and $2\text{--}3^{\circ}\text{C}$.

In the south boreal region where the seasonal vertical migrations of cod are the reverse of those in the north, "optimum" temperatures range from 1.2° to 7.0°C . Uda (1957) suggests that near the western shores of Japan the "optimum" temperatures for cod are between 2° and 4°C . Similar temperatures are recorded by Moiseev (1953: 83) for spawning grounds in the transition areas of southwestern Sakhalin and Peter the Great Bay. Near the southern limit of the cod's range off southeastern Korea, temperatures at depths occupied during summer months do not rise above 6° to 8°C , while winter temperatures are of 5°C or less (Moiseev, 1953: 99—remarks based on the work of Uchida).

It is apparent from the foregoing that Pacific cod in waters along the Asian coast generally are adapted to much lower temperatures than those off the coast of Canada. Only towards the southern limit of the cod's range (Korea) is any similarity of temperature experience to be noted.

In the North Pacific as a whole, cod occur mainly within the range of 0° to 10°C . The pattern of seasonal vertical migration appears to depend on the extent to which temperatures at the extremities of this range intrude upon or envelope the continental shelf. In the Asiatic north boreal region, pronounced migrations of cod to deep water in winter months are accompanied by intensive cooling of the upper zones of the sea (down to 0°C and less). On the other hand, migration to deep water in the summer months in the south boreal region is accompanied by rapid heating of the upper zones to temperatures well above 10°C .

In contrast to these situations we find that off the Canadian coast, seasonal changes in temperature are very moderate and that these are associated with only moderate changes in the seasonal bathymetric distribution of cod.

It is this general association between cod movements and the amplitude and timing of seasonal cycles of temperature which leads one to suspect that temperature *per se* is of over-riding importance in the geographic and bathymetric distribution of cod in the North Pacific.

OTHER BIOLOGICAL CHARACTERISTICS OF PACIFIC COD IN CANADIAN WATERS

In the foregoing section evidence was presented in support of the view that Pacific cod are adapted to conditions of relatively high temperature in waters along the Canadian coast. In such an environment there would be reason to suspect a higher rate of metabolism than in other regions of the North Pacific and that this would manifest in a higher rate of growth, earlier maturity and a

higher rate of natural mortality. It is instructive, therefore, to examine available data on these processes in Canadian cod and compare them with observations from the northwestern Pacific.

A. GROWTH RATE

As yet, no effective method has been developed for age determination of cod taken in Canadian waters. Scales and otoliths (conventional tools for age determination) appear to be unsuitable for they lack well-defined and consistent patterns of annular checks. This in itself may be indicative of a high-temperature environment, for the difficulty of age determination is not encountered to the same degree in age materials collected in colder regions of the North Pacific. Otolith and scale samples from the southeastern Bering Sea (examined by staff of the Nanaimo Station) appear to possess patterns which are representative of age⁸. Also, Mosher (1954) was able to obtain estimates of age from otolith samples collected in the same area.

Otoliths and scales have also been used by Soviet scientists working on cod of the northwestern Pacific. However, age determination of Asian cod appears to require use of both the otolith and the scale, as neither one is satisfactory by itself for all sizes of fish (Moiseev, 1953: 61).

Despite the present lack of satisfactory methods for age determination of cod in Canadian waters, some information on growth rate can be obtained from length-frequency data and from the results of tagging.

1. GROWTH EVIDENT FROM MOVEMENT OF LENGTH MODES

For the purpose of calculations which follow it is presumed that March 1 marks the beginning of the "cod year". In the Strait of Georgia, small-meshed trawl surveys have shown that O-group cod achieve a length of 10.7 cm (range 8 to 14 cm) by mid-July. Growth rate may be somewhat greater in this region than in Hecate Strait (400 miles to the northwest) where young cod have been observed to reach a length of 8.9 cm (range 6 to 11 cm) by the same time of year.

By late autumn in the first year of life, juvenile cod in the Strait of Georgia exceed 20 cm in length. Results of sampling during the winters of 1954-55 and 1957-58 are shown in Fig. 9 (data from Table VII). These data permit an approximate estimate of the length attained at completion of the first year of growth. The average size ($\bar{x}$) and standard deviation (s) of the smallest modal group on November 15, 1954 was $\bar{x} = 20.7$ cm, $s = 1.8$; on January 12, 1955 $\bar{x} = 24.1$ cm, $s = 1.9$. Graphical extrapolation to March 1, 1955, yields an estimate of 26.9 cm. Interpolation from the average size on December 17, 1957 ($\bar{x} = 21.8$ cm, $s = 2.2$) and on March 19, 1958 ($\bar{x} = 26.4$ cm, $s = 2.7$) yields a

⁸These samples have been provided through the cooperation of the staff of the International Pacific Halibut Commission and the U.S. Bureau of Commercial Fisheries (Seattle).

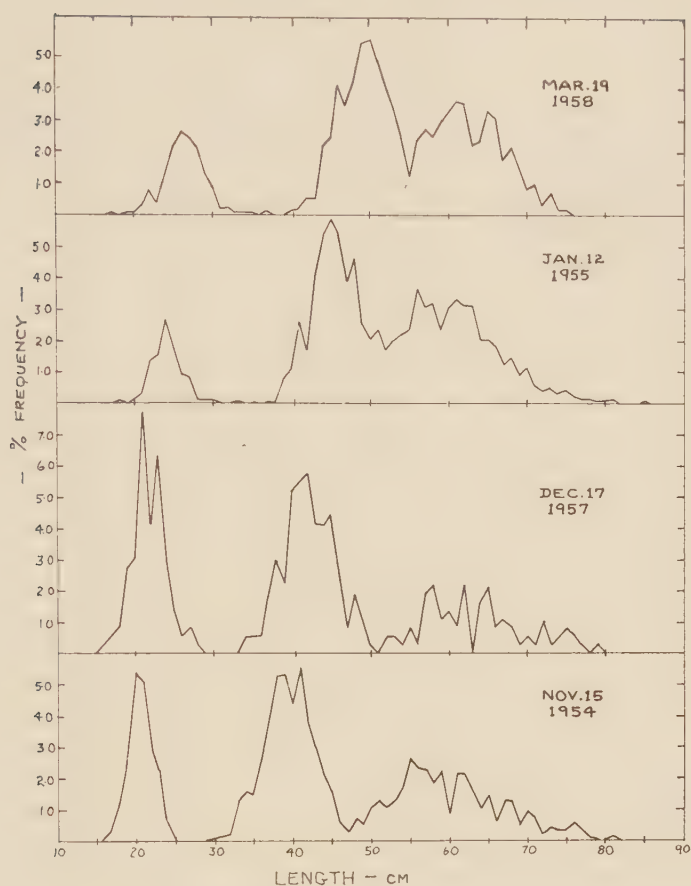


FIG. 9. Length-frequency distributions of Pacific cod taken by the research trawler M/V *Investigator No. 1* on grounds along the east coast of Vancouver Island, Strait of Georgia.

value of 25.4 cm for March 1, 1958. The average of these two estimates is 26.1 cm, which for present purposes shall be regarded as the average length achieved at the completion of the first year of growth (Age I).

As shown in Fig. 9, another mode appears in the length-frequency distribution between lengths of about 40 cm to 50 cm. This group consisted of fish which were in the process of completing their second year of growth. Their separation from still older fish was achieved by plotting the data on probability paper, thus providing the following estimates of average length:

	Nov 15 1954	Dec. 17 1957	Jan 12 1955	Mar 19 1958
Average length (cm)	40.0	42.5	46.4	49.4
Standard deviation (s)	3.0	3.1	3.5	3.1

TABLE VII. Length-frequency distributions of Pacific cod taken on trawling grounds along the lower east coast of Vancouver Island, Strait of Georgia.

Length	Nov. 15, 1954		Dec. 17, 1957		Jan. 12, 1955		Mar. 19, 1958	
<i>cm</i>	<i>no.</i>	<i>%</i>	<i>no.</i>	<i>%</i>	<i>no.</i>	<i>%</i>	<i>no.</i>	<i>%</i>
16	...	...	1	0.27	...	...	...	...
17	4	0.43	2	0.55	...	...	1	0.09
18	11	1.18	3	0.82	1	0.08	...	...
19	22	2.35	10	2.75	...	...	1	0.09
20	51	5.44	11	3.02	2	0.16	1	0.09
21	48	5.12	28	7.70	4	0.33	4	0.35
22	29	3.09	15	4.12	16	1.31	9	0.80
23	22	2.35	23	6.32	19	1.56	4	0.35
24	6	0.64	11	3.02	33	2.71	13	1.15
25	1	0.11	5	1.37	21	1.72	24	2.13
26	...	...	2	0.55	11	0.90	30	2.66
27	...	...	3	0.82	10	0.82	28	2.49
28	...	...	1	0.27	1	0.08	24	2.13
29	...	...	...	...	1	0.08	15	1.33
30	1	0.11	...	...	1	0.08	10	0.89
31	1	0.11	...	...	...	...	2	0.18
32	2	0.21	...	...	...	...	3	0.27
33	12	1.28	...	...	1	0.08	1	0.09
34	15	1.60	2	0.55	...	...	1	0.09
35	14	1.49	2	0.55	1	0.08	1	0.09
36	24	2.56	2	0.55	...	...	...	...
37	38	4.06	7	1.92	1	0.08	1	0.09
38	50	5.34	11	3.02	1	0.08	...	...
39	50	5.34	8	2.20	10	0.82	...	...
40	41	4.37	19	5.22	14	1.15	2	0.18
41	52	5.54	20	5.50	32	2.63	3	0.27
42	34	3.63	21	5.77	20	1.64	6	0.53
43	28	2.98	15	4.12	50	4.11	6	0.53
44	19	2.03	15	4.12	65	5.34	24	2.13
45	15	1.60	16	4.40	72	5.91	27	2.40
46	6	0.64	10	2.75	65	5.34	47	4.17
47	3	0.32	3	0.82	47	3.86	40	3.55
48	7	0.75	7	1.92	57	4.68	48	4.26
49	5	0.53	4	1.10	31	2.55	61	5.41

TABLE VII (continued)

Length	Nov. 15, 1954		Dec. 17, 1957		Jan. 12, 1955		Mar. 19, 1958	
<i>cm</i>	<i>no.</i>	<i>%</i>	<i>no.</i>	<i>%</i>	<i>no.</i>	<i>%</i>	<i>no.</i>	<i>%</i>
50	10	1.07	1	0.27	25	2.05	63	5.58
51	12	1.28	...	...	29	2.38	55	4.88
52	10	1.07	2	0.55	21	1.72	46	4.08
53	12	1.28	2	0.55	25	2.05	38	3.37
54	16	1.71	1	0.27	27	2.24	27	2.40
55	25	2.67	3	0.82	29	2.38	14	1.24
56	22	2.35	1	0.27	45	3.70	27	2.40
57	21	2.24	7	1.92	38	3.12	31	2.75
58	17	1.81	8	2.20	39	3.21	28	2.49
59	21	2.24	4	1.10	29	2.38	33	2.93
60	8	0.85	5	1.37	37	3.04	37	3.28
61	20	2.13	3	0.82	41	3.37	41	3.64
62	20	2.13	8	2.20	38	3.12	40	3.55
63	15	1.60	...	...	38	3.12	25	2.22
64	10	1.07	6	1.65	25	2.05	26	2.31
65	14	1.49	8	2.20	25	2.05	38	3.37
66	6	0.64	3	0.82	23	1.89	34	3.02
67	12	1.28	4	1.10	15	1.23	20	1.77
68	12	1.28	3	0.82	18	1.48	24	2.13
69	5	0.53	1	0.27	11	0.90	17	1.51
70	9	0.96	2	0.55	14	1.15	9	0.80
71	7	0.75	1	0.27	7	0.57	11	0.98
72	2	0.21	4	1.10	5	0.41	4	0.35
73	4	0.43	1	0.27	6	0.49	8	0.71
74	3	0.32	2	0.55	4	0.33	2	0.18
75	3	0.32	3	0.82	5	0.41	2	0.18
76	5	0.53	2	0.55	3	0.25	...	...
77	3	0.32	1	0.27	2	0.16	...	...
78	1	0.11	...	...	2	0.16	...	...
79	...	...	1	0.27	1	0.08	...	...
80	...	...	...	...	...	...	...	...
81	1	0.11	...	...	2	0.16	...	...
82	...	...	...	...	...	...	...	...
82	...	...	...	...	...	...	...	...
84	...	...	...	...	...	...	...	...
85	...	...	...	...	1	0.08	...	...
Total	937		364		1,217		1,127	

As in the computation of average length at Age I, the November and January average lengths were extrapolated to March 1, yielding an estimate of 51.9 cm; the December and March averages were interpolated to obtain an estimate of 47.9 cm. The mean of these two estimates is 49.9 cm, and is here taken as an approximation of the length attained at the completion of Age II.

Although this group can be traced well into its third year of growth, overlapping with older age groups increases and makes difficult a reliable separation of the length-frequency distribution into its component parts.

2. GROWTH EVIDENT FROM TAGGING

An alternative procedure for determining growth rate of Age II and older fish is to be found in the results of tagging. As noted above, average length at completion of Age II was estimated to be 49.9 cm. If we ascribe to the frequency distribution of these fish a standard deviation of 3.2 (an average from the foregoing table), we can say that the majority of Age II fish were within the range 46.7–53.1 cm.

From 1954 to 1959 inclusive, 6,075 Pacific cod were tagged on Strait of Georgia grounds and all were released during the winter period. Within the range 46.7 to 53.1 cm, 67 fish, for which reliable information was available on growth, were recaptured one year after tagging (actually, the 11th to 13th month after release). The average length of these fish, when tagged, was 49.6 cm—for practical purposes, the same as that estimated as average length of fish which had completed Age II. The average length at recapture was 61.4 cm ($s = 4.2$) which can be taken as an approximation of the length at completed Age III. Unfortunately, recaptures after two years of freedom were so few that it was impossible to estimate length at completed Age IV from this particular group of tagged fish.

However, as an alternative, we can examine the one-year returns from fish tagged at the size estimated for Age III fish above, namely, within the range 57.2 to 65.6 cm. A total of 76 fish qualified for this treatment, and their average length at time of recapture was 66.1 cm ($s = 3.8$). However, their average length at time of tagging was only 60.3 cm, as compared with the 61.4 cm as estimated above for length at completion of Age III. Therefore, an approximate correction for the average length at completed Age IV would be $61.4 \times 66.1 / 60.3$ or 67.3 cm.

Of course, these are rather hazardous calculations, and they become increasingly so as we attempt to determine average lengths for the few remaining ages in the life span. Not only are the numbers of eligible tag recoveries fewer but the sex ratio beyond Age IV swings strongly in favour of female fish which presumably grow more rapidly than male fish⁹. Thus, the apparent growth rate may accelerate as the numbers of males decrease among larger fish. Further-

⁹In these growth studies based on tagging data, growth rates could not be determined for male and female fish separately. At time of tagging there is no means of determining sex, and recaptured fish are usually gutted before they are reported.

more, from Age IV onwards the standard deviations of the length distributions for the various age groups begin to overlap.

Twenty-seven tagged fish within the length range 63.5 to 71.1 cm (i.e., as Age IV with mean size 67.3 cm, $s = 3.8$) averaged 71.6 cm in length ($s = 3.8$) one year later. Again, correcting for the disparity between the actual mean length at time of tagging (66.3 cm) and that calculated for Age IV, we get $67.3/66.3 \times 71.6 = 72.6$ cm as the estimated length at Age V.

Ten fish tagged within the range 68.8–76.4 cm (Age V, 72.6 ± 3.8 cm) had an average length of 75.1 cm one year later. Their average length at time of tagging was, however, 71.5 cm. Thus, the corrected estimate of the average length at Age VI was $72.6/71.5 \times 75.1$ or 76.2 cm.

Beyond this point no further information is available because of the paucity of one-year returns from taggings of fish greater than 72 cm in length.

The foregoing calculated lengths at each age are summarized in Table VIII with estimates of the apparent average annual increment (as well as estimates of average weight and instantaneous growth rate). Data from columns 2 and 3 of this table are illustrated in Fig. 10, part (b) of which is a modification of the Walford-type relationship between length at time of tagging (l_t) and length one year after tagging (l_{t+1}). In this case, the annual increment of growth in length ($l_{t+1} - l_t$) is plotted against l_t , a graphical expression of the modified Brody-Bertalanffy equation:

$$l_{t+1} - l_t = L_{\infty}(1 - e^{-K}) + l_t(e^{-K} - 1)$$

where K is the growth coefficient and L_{∞} is the asymptotic length (see Holt, 1959).

A least-squares fit to all of the data in Fig. 10b (solid line) yields $K = 0.58$ and $L_{\infty} = 77.4$ cm, whereas, if we consider only the first three points as being reliable (broken line in Fig. 10b), then $K = 0.71$ and $L_{\infty} = 72.8$ cm.

The suggestion mentioned by Ricker (1958: 195) for obtaining a better fit (by using trial values of L_{∞} to find the straightest (best) line fitting the plot of values of $\log_e(L_{\infty} - l_t)$ against t) could be followed. However, in view of the questionable accuracy of the data, it might be more appropriate simply to fit by eye a line which provides a value of L_{∞} intermediate to those given above, i.e., $L_{\infty} = 75.1$, whence K is found to be 0.67.

Alternatively, we may treat the tagging data less selectively by avoiding any separation into age groups. Thus in Fig. 11, increments of growth as indicated by all one-year tag returns are plotted against lengths at time of tagging. The line of best fit to these data is expressed as $Y = 324 - 0.432 X$, whence it follows that $K = 0.56$ and $L_{\infty} = 75.0$. Although these values are in close accord with those derived from Fig. 10b, the limits of error are obviously quite large. The high degree of variability in values of $l_{t+1} - l_t$ is generated at least in part by differential rate of growth between the sexes. As mentioned earlier, it was not possible to separate the tag returns by sex. Furthermore, it is fairly obvious

TABLE VIII. Estimated growth rate of Pacific cod in Strait of Georgia waters, based on observations of length-frequency modes and on results of tagging.

1	2	3	4	5	6	7
Age (completed years)	Average length	Average increment	Average weight		Log _e (wt)	Instantaneous growth rate (g)
I	cm 26.1	cm 23.8	g 200	lb 0.45	5.30	1.99
II	49.9	11.5	1,470	3.23	7.29	0.64
III	61.4	5.9	2,780	6.15	7.93	0.25
IV	67.3	5.3	3,570	7.87	8.18	0.19
V	72.6	3.6	4,330	9.55	8.37	0.18
VI	76.2		5,180	11.42	8.55	

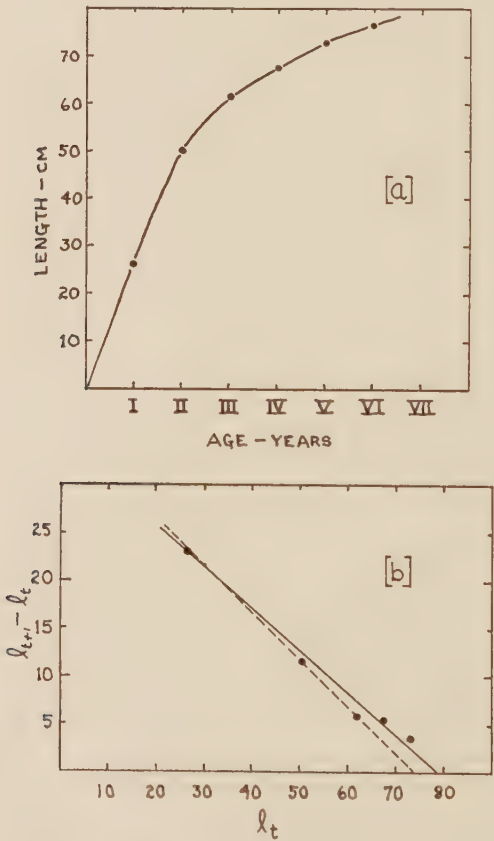


FIG. 10. Estimated growth of Pacific cod in the Strait of Georgia: (a) relation between length and age, and (b) the same data expressed as a modified Walford graph.

in Fig. 11 that the relationship between $l_{t+1} - l_t$ and l_t would be better described by a curvilinear expression rather than a linear one.

Accordingly, it must be recognized that the values of K and L_∞ as computed here, and used in a later section dealing with mortality rates, are merely approximations. Further work appears necessary in order to determine whether or not the growth rate of Pacific cod in Strait of Georgia waters is described with sufficient accuracy by the Brody-Bertalanffy equation.

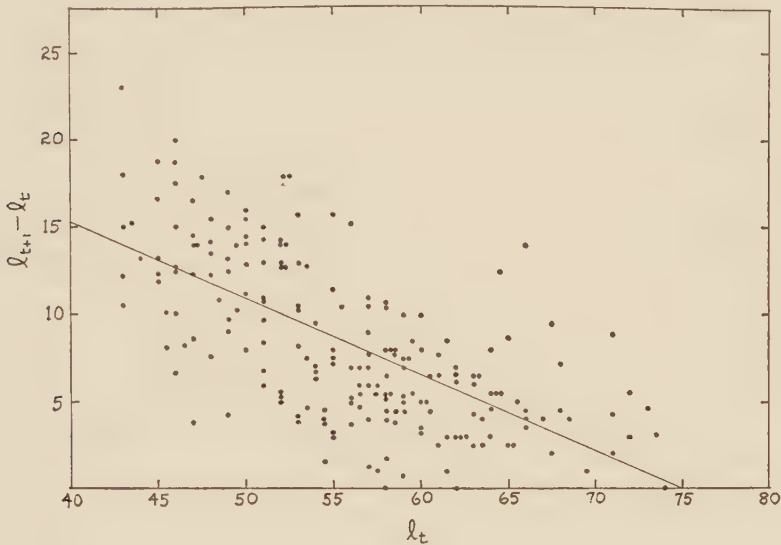


FIG. 11. A modified Walford graph showing the relation between length of Strait of Georgia cod at time of tagging (l_t) and the increment of growth after one year at large ($l_{t+1} - l_t$). Measurements in centimetres.

Further work is also required to determine whether or not the growth rate as exhibited by Strait of Georgia fish differs significantly from that in the open waters of the Canadian coast (Hecate Strait, Queen Charlotte Sound, etc.). Preliminary tagging in the Strait of Georgia (Forrester and Ketchen, 1955) resulted in only a few recaptures being made in outside waters (west coast of Vancouver Island). Subsequent taggings have revealed more emigration, but the weight of evidence still favours the conclusion that Strait of Georgia cod are more or less independent of those offshore. Nevertheless, length-frequency distributions for all areas are very similar and this would suggest that growth rate and age composition is not markedly different between inshore and offshore grounds, at least adjacent to the southern Canadian coast. As mentioned earlier, growth rate in northern (Hecate Strait) waters may be slightly slower than in the south—and this might be expected in view of the temperature difference between the two areas. Results of recent taggings in Hecate Strait must be awaited before this question can be answered with certainty.

It is instructive to compare the above observations on growth rate of Strait of Georgia cod (approximate as they may be) with similar observations in the northwestern Pacific Ocean. Such a comparison is made in Fig. 12 (data from Table IX). Information respecting cod of western Bering Sea and the Sea of Okhotsk (west Kamchatka) is taken from Moiseev (1953: 66) and is based on back calculations. Data for the east coast of Korea were obtained indirectly

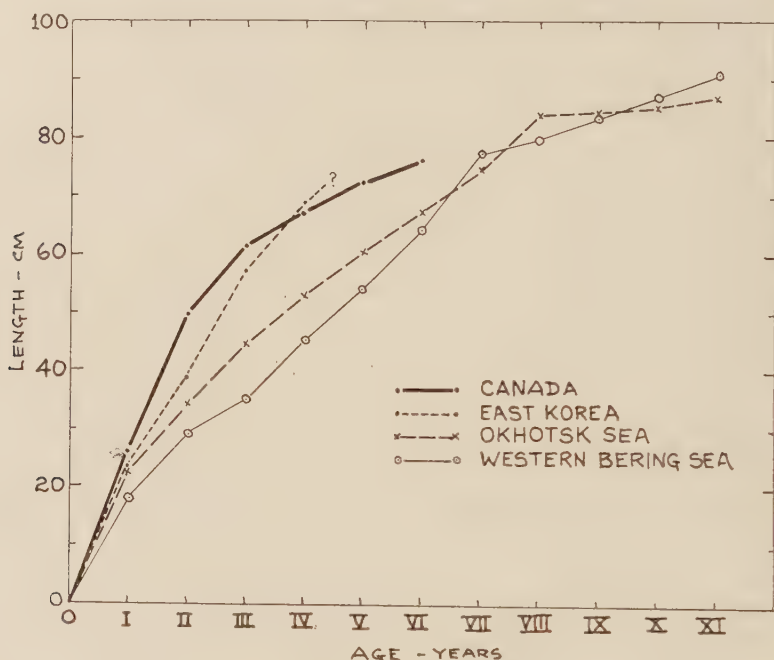


FIG. 12. A comparison of the age-length relationships of cod inhabiting various regions of the North Pacific Ocean and adjoining seas.

TABLE IX. Age-length relationships of cod from various regions of the North Pacific Ocean and adjoining seas.

	Average length (cm) at ages below (completed years)										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1. West Bering Sea (1933 Olyutorski Bay)	18.0	29.5	35.5	45.7	54.2	64.2	77.4	79.8	83.6	87.0	91.0
2. Sea of Okhotsk (1929-33)	22.8	34.6	44.8	53.4	60.8	67.7	75.1	84.0	84.1	85.5	87.5
3. East coast of Korea											
Range	20-27	30-48	50-65	66-72	ca 80	ca 90					
Mid-point	(23.5)	(39.0)	(57.5)	(69.0)							
4. British Columbia (Strait of Georgia 1954-58)	26.1	49.9	61.4	67.3	72.6	76.2	?				

from a paper by Uchida (1936)¹⁰. As Uchida gave only the range of lengths at each age, a mean point in the range has been used in drawing the graph shown in Fig. 12.

Strait of Georgia cod appear to have a more rapid initial rate of growth than those in the three other areas considered (presuming that data for the latter are representative of present-day conditions). Although there is some uncertainty about the accuracy of the estimates beyond Age III, growth rate beyond this age becomes less than that observed in the Sea of Okhotsk and western Bering Sea. Up to Age III the rate of growth of Canadian cod is closer to that in Korean waters than in the regions farther to the north whose temperatures are less similar to Canadian waters.

For comparison, the southernmost stock of Atlantic cod along the American coast occurs off southern New England between 35° and 41°N Lat. (Wise, 1958)—much the same as the latitudes occupied by cod at the southern limit of their range in Asia (Korea). For southern New England cod, Schroeder (1930, table 44) gives the following average lengths at each age, as based on back-calculations from scale measurements:

I	17.0 <i>cm</i>	VI	78.0 <i>cm</i>
II	38.4	VII	85.3
III	52.8	VIII	91.7
IV	63.0	IX	98.3
V	70.4	X	104.2

For the first two years of age the growth rate shown is much less than that of British Columbia cod, but perhaps about the same as in Korean waters.

B. MORTALITY RATES

Because of uncertainties encountered in age determination, conventional methods of determining total mortality rate from age composition have not as yet been applied to Pacific cod in Canadian waters. Accordingly, it is necessary to rely *pro tem* on other sources of information.

1. MORTALITY RATE AS RELATED TO AVERAGE LENGTH

Where information is available on growth rate and average length of fish in the catch, an approximation can be obtained of total mortality rate. In terms of the Brody-Bertalanffy growth formula, Beverton and Holt (1956: 69) derived the following expression

$$i = \frac{K(L_{\infty} - \bar{l})}{\bar{l} - l'}$$

where i is the instantaneous total mortality (Beverton and Holt's $F + M$), $\bar{l}$ is the average length of fish in the catch that are as large or larger than the first fully recruited length, l' .

¹⁰I am indebted to Mr F. Nagasaki of the Tokai Regional Fisheries Research Laboratory, Tokyo, Japan, for his help in abstracting pertinent information from Uchida's paper.

Within the area for which information is available on growth rate of cod (southern Strait of Georgia), one of the main fishing grounds is that at Nanoose Bay. The fishery takes place on spawning or pre-spawning concentrations of cod during the months of February and March. Routine sampling for length has been conducted on commercial trawler catches from this ground for about a decade. The average length-frequency distribution for the years 1956-60 is given in Table X.

TABLE X. Average length-frequency distribution of Pacific cod in 1956-60 trawl catches from the Nanoose Bay fishing ground in the Strait of Georgia.

Length	Frequency	Length	Frequency	Length	Frequency
cm	%	cm	%	cm	%
40	...	55	4.44	70	1.70
41	0.16	56	5.82	71	1.30
42	0.36	57	6.36	72	0.82
43	0.50	58	7.32	73	0.98
44	0.44	59	6.38	74	0.56
45	0.80	60	6.82	75	0.46
46	1.02	61	6.28	76	0.22
47	1.24	62	5.64	77	0.18
48	1.40	62	5.78	78	0.09
49	1.48	64	4.08	79	0.09
50	1.86	65	3.86	80	0.09
51	1.82	66	3.14	81	...
52	2.54	67	2.96	82	0.04
53	2.66	68	2.58	83	0.04
54	3.86	69	2.02	84	...

When the data are smoothed (by threes) it appears that the mode is situated at about 59 cm. To allow for still incomplete recruitment, we may estimate l' as 60.0 cm, whence it follows that $\bar{l}$ is 64.6 cm.

These values are now applied to the above expression together with the various estimates of K and L_{∞} evolved on page 539. The results are as follows:

Source	K	L_{∞}	i	a
1 Fig. 10b	0.58	77.4	1.62	.802
2 " "	0.71	72.8	1.27	.719
3 " "	0.67	75.1	1.53	.784
4 Fig. 11	0.56	75.0	1.27	.719

In all cases the estimates of i (or a , the annual total mortality rate) are remarkably high as high as estimates obtained from *heavily fished stocks of Pacific herring* (cf. Tester, 1955: 666). Of course, their reliability hangs heavily on the accuracy of estimates of K and L_{∞} , and small differences in these latter values result in a considerable difference in estimates of i (cf. i_1 and i_4).

Ricker (1958: 204) suggests that the greatest weakness of mortality estimates based on average length is that they do not detect possible age variation in

mortality rate. As will be shown in the discussion of mortality estimates from tagging, the mortality rate of Strait of Georgia cod (or at least the rate of disappearance from the fishery) seems to increase with age. This may limit the usefulness of the Beverton and Holt expression (which assumes i to be constant) even if wholly reliable data on growth rate were at hand.

A high apparent total mortality rate *might* reflect not only the rate of death due to fishing and natural circumstances but also a certain rate of permanent emigration from the effective range of fishing. Actually this is rather improbable. Canadian and United States trawler fleets operate over a range of depths which extend well above and below the depths where cod are to be found. Catches are fairly homogeneous with respect to length, and little segregation by size amongst mature fish can be detected such as would appear if the fish moved to deeper water as they got larger and older (as do blackcod, lingcod and other species).

Despite markedly different histories of exploitation, the length-frequency compositions of cod from various banks along the Canadian coast are very similar. Hence, the preliminary conclusion is that total mortality rate is of the same order of magnitude in all areas and that a large share of this is due to natural mortality. Samples collected from northern Hecate Strait in 1951, when the cod fishery was in its early stages of development, indicated a total mortality rate in excess of 60% per annum (based on the Beverton-Holt method described above). Thus, it is conceivable that annual natural mortality rate is of the order of 60% (about 0.9 on an instantaneous basis).

2. MORTALITY RATES BASED ON TAG RETURNS

Mature cod move in to the Nanoose Bay ground, Strait of Georgia, during the months of February and March, from southern waters of the Strait. Fishing is restricted by regulation to the period February 1 to March 20 each year. In 1955 and 1958 tagging was conducted toward the end of the open season in Nanoose Bay (Table XI). In both years, during the first 6 months after tagging relatively few recaptures were made—partly because of cessation of fishing in the tagging area and partly because of reduced fishing effort in other parts of the Strait of Georgia during the spring and summer months. The bulk of the returns came in the 7th to 12th months and within that period most came during the 11th and 12th months on the Nanoose Bay ground.

Survival rates, based on first and second year recaptures from each tagging are shown in the following tabulation. Allowance for differences in fishing effort (Table XII) has been made in the adjusted second year recaptures.

Year of tagging	1st year recaps	2nd year recaps	Adjusted 2nd year recaps	Survival rate s	Inst. total mortality rate i
1955	82	12	14	.171	1.77
1958	43	11	10	.233	1.46

TABLE XI. Recaptures from cod tagging conducted at Nanoose Bay in March 1955 and March 1958. Column 1 indicates size range at tagging.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
Length group (cm)	1955 tagging						1958 tagging						Combined taggings			
	Numbers tagged		Numbers of recaptures				Numbers tagged	Numbers of recaptures				Numbers tagged	Numbers of recaptures			
			1-6 mo.	7-12 mo.	13-18 mo.	19-24 mo.		1-6 mo.	7-12 mo.	13-18 mo.	19-24 mo.		1-6 mo.	7-12 mo.	13-18 mo.	19-24 mo.
<41	2	...	...	...	...	...	...	...	...	...	2	...	...	...	...	
41-45	7	...	1	...	...	10	...	...	...	...	17	...	1	...	...	
46-50	25	...	3	...	...	71	2	5	...	...	96	2	8	...	...	
51-55	65	3	8	...	3	95	3	3	...	1	160	6	11	...	4	
56-60	171	4	19	2	1	161	2	12	1	1	332	6	31	3	2	
61-65	177	5	21	1	2	188	3	6	...	1	365	8	27	1	3	
66-70	117	6	5	...	...	106	4	1	...	...	223	10	6	...	...	
71-75	44	2	5	3	...	27	1	1	...	...	71	3	6	3	...	
76-80	8	...	...	...	...	5	...	...	...	...	13	...	...	...	...	
>80	3	...	...	...	...	1	...	...	...	...	4	...	...	...	...	
Unclassified		...	...	...	...		...	...	...	(7)		...	...	...	(7)	
Totals	619	20	62	6	6	664	15	28	1	(10)	1,283	35	90	7	(16)	
		82			12		43			(11)			125		(23)	

TABLE XII. Statistics of total fishing effort (hours of trawling) in the southern part of the Strait of Georgia.

Area	Year and period							
	1955	1955-56	1956	1956-57	1958	1958-59	1959	1959-60
	Apr- Sept	Oct- Mar	Apr- Sept	Oct- Mar	Apr- Sept	Oct- Mar	Apr- Sept	Oct- Mar
Gulf Islands	1,519	5,364	2,150	4,089	1,086	4,493	1,001	4,957
Nanoose Bay	...	462	...	327	...	507	...	732
Totals	1,519	5,826	2,150	4,416	1,086	5,000	1,001	5,689
	7,345		6,566		6,086		6,690	

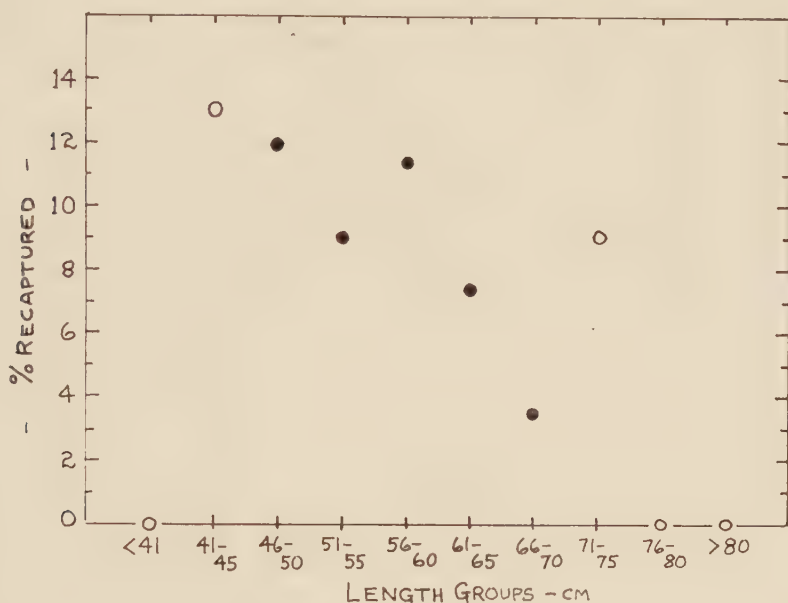


FIG. 13. Percentage returns from various tagged length groups of cod, 7 to 12 months after tagging at Nanoose Bay, Strait of Georgia (data from Table XIV). Open circles indicate recaptures from fewer than 100 tagged fish.

This analysis probably puts an upper limit on the estimates of i . Some allowance was made for the loss of tags through shedding, but this factor could not be corrected for entirely. Shedding is known to have occurred in the tags used at Nanoose Bay, particularly in 1958¹¹. In addition, the observed decrease in tag returns with size (Fig. 13) suggests a bias in the direction of greater than

¹¹Since 1955, various types of tags have been used: polyvinyl (spaghetti) tubing, monofilament and braided cord of nylon and other synthetics. In 1958, only polyvinyl tubing was used at Nanoose Bay. No shedding was apparent until the second year when a number of broken tags were reported (the "unclassified" tags in Table XI). Although these lacked identifying serial numbers, it was presumed that they originated from the 1958 tagging. These broken tags were still fused to the fish when captured. Presumably others did not remain attached.

representative mortality because the fish were two years older by the time the final returns were in.

A weighted average of the two estimates of i (1.68) was obtained by pooling the first and second year recaptures from the two taggings and weighting these to the pooled fishing effort.

In spite of the likelihood that this is an overestimate of total mortality rate, it is instructive to consider briefly a method of partitioning the component rates of fishing and natural mortality, based on the hypothesis that (1) natural mortality is at a uniform instantaneous rate throughout the year, and (2) that the instantaneous rate of fishing mortality varies as fishing effort throughout the year. Dr W. E. Ricker has suggested the following procedure:

Combined first-year recaptures from the 1955 and 1958 taggings are assembled by quarter-year periods (1 to 4) in Table XIII, together with data on total fishing effort (from Table XII).

TABLE XIII. First-year tag returns by quarters from the March, 1955 and March, 1958 cod taggings at Nanoose Bay and associated statistics of fishing effort for the southern part of the Strait of Georgia.

	Period			
	1	2	3	4
	Apr-Jun	Jul-Sept	Oct-Dec	Jan-Mar
Tag returns				
1955 tagging	11	—	8	18
1958 tagging	18	6	16	48
Totals	29	6	24	66
Hours of fishing	35		90	
1955	1,519		5,826	
1958	1,086		5,000	
Total	2,605		10,826	

Fishing effort in the first two periods $f_{1+2} = 2,605$ hours, and $f_{3+4} = 10,826$ hours. On the basis of the ratio of recaptures in periods 3 and 4, i.e., 24:66, we estimate that $f_3/f_4 = 1/2.75$, whence $f_3 = 2,887$ hours and $f_4 = 7,939$ hours¹².

Assuming that hours of fishing measure effective effort, then the instantaneous rate of fishing mortality is proportional to fishing effort (f). Hence:

$$\frac{p}{13431} = \frac{p_1 + p_2}{2605} = \frac{p_3}{2887} = \frac{p_4}{7939}$$

¹²It would have been better to use the actual fishing effort by quarters but these statistics were not readily available.

If we take a trial value $q = 1.20$ for the instantaneous natural mortality rate, then the corresponding trial value of p is $1.68 - 1.20$ or 0.48 . Thus for Periods 1 and 2 we have the following:

$$\text{trial } p_1 + p_2 = \frac{2605}{13431} \times 0.48 = 0.09$$

$$\text{trial } q_1 + q_2 = \frac{1.20}{2} = 0.60$$

$$\text{trial } i_{1+2} = 0.09 + 0.60 = 0.69$$

The expected recaptures in Periods 1 and 2 are equal to the number tagged multiplied by:

$$(p_1 + p_2) \frac{a_{1+2}}{i_{1+2}}$$

In this particular case, 1,283 cod were tagged. Of this number, 93% (1,193) were classed as being in good condition at time of tagging. This number will be used as an approximate correction for initial tagging mortality. Thus, using the trial values above:

$$\text{Expected recaptures} = 1193 \times 0.09 \times 0.7224 = 78$$

From this it follows that at the end of Period 2 the survivors, S_2 , are:

$$S_2 = 1193 \times e^{-i_{1+2}} = 598$$

For Period 3:

$$\text{trial } p_3 = \frac{2887}{13431} \times 0.48 = 0.10$$

$$\text{trial } q_3 = \frac{1.20}{4} = 0.30$$

$$\text{trial } i_3 = 0.40$$

$$\text{Expected recaptures} = S_2 \cdot p_3 \cdot \frac{a_3}{i_3} = 49$$

$$\text{Survivors} = S_3 = 598 \times e^{-i_3} = 401$$

Similarly, for Period 4:

$$\text{trial } p_4 = \frac{7939}{13431} \times 0.48 = 0.28$$

$$\text{trial } q_4 = \frac{1.20}{4} = 0.30$$

$$\text{trial } i_4 = 0.58$$

$$\text{Expected recaptures} = S_3 \cdot p_4 \cdot \frac{a_4}{i_4} = 85$$

Under this scheme (using trial $q = 1.2$) $78 + 49 + 85$ or a total of 212 recaptures would be expected during the first year. The actual number, however, was $35 + 24 + 66$, or 125.

Trials with other values of q soon lead to an approximation of this latter number. Thus, when $q = 1.39$ (and $p = 0.29$) the expected number of recaptures was 126. However, the seasonal distribution could be duplicated with only partial satisfaction (47, 29 and 50).

Of course this high value of q (1.39, or 75% expressed as an annual rate) is probably a maximum estimate. Initial tagging mortality, incomplete correction for unreported tag recaptures and tag loss through shedding all lead to underestimation of p , while the last-named factor leads to overestimation of i ; hence $q (=i-p)$ tends to be overestimated.

Values of i obtained by the two separate taggings of 1955 and 1958 were 1.77 and 1.46, respectively. Although seemingly quite high, they were of about the same order of magnitude as those determined from the average size of fish in the catch (p. 544). While some confidence is to be gained from this agreement, it is possible that the latter method too may embody sources of error which overestimate the total mortality coefficient.

Mention was made previously of the possibility that total mortality rate of cod may vary with age, and hence may render unsuitable the Beverton-Holt method for estimating total mortality rate from length-frequency distribution. It seems worthwhile to examine the evidence on this point before proceeding to other subjects.

Table XIV summarizes the first year returns by length groups from tagging conducted at Nanoose Bay in March of 1955, 1958 and 1959. The numbers of tagged fish in each length group which were recaptured during the first 6 months after tagging were subtracted from the numbers tagged to obtain an estimate of the maximum number at large at the beginning of the 7th month. Recaptures during the 7th to 12th months were then expressed as a percentage of the maximum number at large and plotted in Fig. 13. While there is a limited range of size

TABLE XIV. Summary of first-year returns from taggings of Pacific cod at Nanoose Bay in the month of March in 1955, 1958 and 1959.

1	2	3	4	5	6
Length group (cm)	Number tagged	Recaptures 0-6 months	Max. at large beginning of 7th month	Recaptures 7-12 months	Col 5 Col 4
<41	5	0	5	0	0
41-45	23	0	23	3	0.130
46-50	132	6	126	15	0.119
51-55	318	11	307	28	0.091
56-60	622	14	608	70	0.115
61-65	485	11	474	35	0.074
66-70	247	0	247	9	0.036
71-75	80	2	78	7	0.090
76-80	15	0	15	0	0
>80	4	0	4	0	0
Total	1,931	44	1,887	167	0.089

groups possessing sufficient data, a downward trend in percentage recaptures is evident in size groups greater than 41–45 cm. At present there is no way of differentiating between the size-related effects of (1) decreasing availability to the fishery and (2) increasing natural mortality rate. However there is a lack of evidence of permanent emigration from the fishery (p. 545) and, although its occurrence may be difficult to detect, one is left with the suggestion that natural mortality rate increases with age.

C. AVERAGE AND MAXIMUM LENGTHS OF COD

The Pacific cod is of relatively small size in the southern part of its range along North America. This is one reason why the salt fish fishery of the early days (which depended on large fish) failed to develop closer than it did to ports of landing in the United States. Cobb (1927: 389, 400) makes note of the small size of cod on banks from Kodiak Island southeastward to Dixon Entrance.

In Canadian waters the largest cod ever caught, according to Clemens and Wilby (1946), was 3 feet 3 inches in length (about 99 cm). The largest fish recorded in sampling conducted by the Fisheries Research Board during the past decade was 93 cm (two specimens taken on the Goose Island Bank in May, 1955, between depths of 36–57 fathoms). Another specimen 91.5 cm in length and weighing 21.8 lb (round) was captured off the estuary of the Fraser River in February, 1955. Such records are very rare and, indeed, specimens greater than 80 cm in length are rather uncommon. The length-frequency distribution given in Table X is rather typical of the trawl catches from Canadian waters. The modal length is usually in the vicinity of 60 cm (approximately 6 lb round wt) which, as mentioned earlier, is approximately the length achieved by 3 years of age.

It is evident from the comments of Cobb (1927: 388, 444) that cod taken in the early days by the line fishery in western Alaska were of substantially larger size than those taken in Canadian waters. Average round weight in the catch during a 4-year period was 11.25 lb (average length probably between 75 and 80 cm). Largest specimen recorded by Cobb was one weighing 40 lb and measuring 43 inches (about 110 cm) in length.

For waters of the northwestern Pacific, Moiseev (1953: 45) states that cod do not exceed a length of 115 cm and a weight of 18 kg (about 40 lb), and he points out that Pacific cod do not achieve as large a size as Atlantic cod. According to Moiseev's table 10, the average length of cod taken with various types of fishing gear in western Kamchatka waters between 1929 and 1939 was 78.9 cm—probably rather similar in size composition to the cod which were the object of fishing in western Alaska waters in early days.

The foregoing remarks are intended merely as a general comparison of the sizes of cod in various sectors of the North Pacific. Detailed comparisons are not possible because of the different histories of exploitation and different types of gear used.

D. LENGTH AND AGE AT MATURITY

In Strait of Georgia waters, male and female cod reach sexual maturity at different length and age. Fifty per cent of male fish reach maturity at a length of 48 to 49 cm, which corresponds to an age of 2 (completed) years. Apparently all are mature by 3 years. Only 15% to 25% of female fish are mature by the time they reach Age II, but almost all are mature at Age III. The 50% maturity level is at 55 cm.

Recent studies in northern Hecate Strait showed that 50% of male fish were mature at 49 to 50 cm, while the 50% level was at 55 cm in females—essentially the same as that observed in the Strait of Georgia.

In contrast, cod inhabiting waters off the west coast of Kamchatka (Sea of Okhotsk) mature at a much greater size and age. Calculations based on data presented by Moiseev (1953: table 41) suggest that 50% of male cod are mature at about 70 cm, with a corresponding length of 73 cm for females. These lengths correspond to Age VI (Moiseev's table 42). Moiseev states that the earliest age at which cod reach sexual maturity is 5 years, and that some are still immature at Age IX.

Information available from the work of Uchida (see footnote 10) implies that the cod of eastern Korea first reach maturity at Age III and that the majority are mature by Age V. If so, there is further evidence to suggest that Pacific cod in Canadian waters are biologically more comparable to those of Korean waters than those in the north boreal region of the Asian coast.

E. REPRODUCTIVE POTENTIAL

Although information is lacking which would allow quantitative determination of relative abundance of cod in various regions, it appears that they occur in lesser numbers in Canadian waters than in colder regions to the northwest. Similarly along the Asian coast, abundance apparently decreases from north to south. Conceivably, one reason would be that progressing southward from the region of maximum abundance, environmental conditions become decreasingly favourable for survival of the eggs and larvae. Alternatively, or more likely additionally, there might be a decrease in the reproductive potential—that is, a decrease in the number of eggs spawned per given number of mature fish. Thus the reproductive advantage gained by early maturity in Canadian waters above might be offset by (1) the short life span and (2) a relatively small number of eggs produced per fish at first maturity, if we presume that fecundity is a function of body weight.

In Table XV the length-frequency distribution of 1,000 mature female cod from Nanoose Bay (considered to be fairly typical of spawning populations off the Canadian coast) is compared with that of a similar number of mature females from waters off the west coast of Kamchatka. Data for the latter were obtained from Moiseev (1953: Table 41).

TABLE XV. Length-frequency distribution (per mille) in a typical spawning stock of female Pacific cod in Canadian waters (NanOOSE Bay) as compared with that in waters off the west coast of Kamchatka (the latter adapted from Moiseev 1953: table 41).

Length group cm	Frequency		Length group cm	Frequency	
	NanOOSE Bay	West Kamchatka		NanOOSE Bay	West Kamchatka
40-44	2	...	75-79	19	164
45-49	13	...	80-84	4	124
50-54	46	...	85-89	...	144
55-59	305	16	90-94	...	136
60-64	335	32	95-99	...	64
65-69	194	100	100-104	...	8
70-74	82	212			

As yet no information has been obtained on the fecundity of cod in Canadian waters, so in order to compare the reproductive potentialities of the two groups, it is necessary to assume that the fecundity-length relationship in the two regions is about the same, and employ data provided by Moiseev (his table 51). These data, although few in number, provide the following expression of the relationship between fecundity and total length:

$$\hat{Y} = 0.0135X + 5.370$$

where X is the fish length in cm, and $\hat{Y}$ is the $\log_{10}$ of the number of eggs.

With the aid of length-frequency data for the two areas, it is now possible to estimate the fecundity of the two groups of fish, viz, 1.64×10^9 eggs for the Strait of Georgia (NanOOSE Bay) and 2.93×10^9 eggs for western Kamchatka. Thus, for a given number of mature fish the potential egg production of Kamchatka fish is almost twice as great as that of Strait of Georgia fish—and this can be attributed to the larger size at first maturity and the longer life span.

The assumption that the fecundity-length relationship computed above for Kamchatka waters applies to Strait of Georgia cod is, of course, rather critical. According to Beverton and Holt (1957: 62), egg size within most marine fish seems remarkably constant, but there may be some exceptions (and also exceptions to the rule that fecundity is approximately proportional to body weight). In the light of Moiseev's data, it would appear that the Pacific cod, at least in the region of Asia, is one of these exceptions. A simple proportionality between fecundity and weight is not evident and apparently egg size is not constant from area to area. Moiseev presents data (his table 52) which suggest that cod of given weight (or length?) in waters off western Sakhalin produce 1.5 to 1.9 times as many eggs as cod from western Kamchatka. In this regard, Moiseev (p. 77) quotes a rule propounded by Rass (1941) to the effect that size of the cod egg increases to the northward and hence the number of eggs produced per given fish weight decreases.

The need for a test of this rule in the northeastern Pacific is apparent. If egg number per unit weight of fish (or weight of ovary) varies with latitude by

as much as a factor of 1.5 to 1.9, then it is possible that the difference in reproductive potential suggested in the discussion of Table XV would be largely negated. It remains to be determined whether or not the size of egg (and hence numbers of eggs) produced by cod in Canadian waters effectively compensates for the small size at maturity and the relatively short life span.

DISCUSSION

Although much remains to be learned about the biology of the Pacific cod in Canadian waters, it is evident that this particular geographic race or population is adapted to relatively high environmental temperatures. Furthermore, and in accordance with what can be regarded as a general rule, cod in Canadian waters are smaller than their kin in cooler regions of the North Pacific, but at the same time their growth rate in the first few years of life is more rapid. These fish mature at a relatively early age and appear to have a high annual death rate, much of which probably can be attributed to natural causes. Amongst commercially important representatives of the genus *Gadus* (viz. *G. morhua*, *G. macrocephalus*) these are unusual characteristics deserving further study and more accurate description.

Recently, Beverton and Holt (1960: 164) made a preliminary attempt to establish a relationship between the growth coefficient K and the natural mortality coefficient M (or q , as used in this paper) for the Gadiformes and other groups of fishes. Although data for the gadiform fishes (cod, haddock, coalfish, hake, etc.) are rather sparse, it appears that if we apply the K values of 0.56 to 0.71 (from page 544) to Beverton and Holt's figure 6, estimates of q are obtained which range from about 1.3 to 1.7. Beverton and Holt attach no statistical significance to their line relating values of K and q , but the above values (1.3–1.7) of q for Pacific cod in Canadian waters bracket the estimate obtained from tagging data ($q = 1.39$, from page 550). Because of errors inherent in the tagging method the latter estimate must still be regarded as too high, but the primitive length composition data suggest that the true figure could be as high as 0.9 at least.

Further confirmation of the relatively high value of K and q will be required before detailed consideration can be given to their significance in fishery management. However, if the preliminary results are of the right order of magnitude, it is apparent without recourse to population models that maximum yield from a year-class will be achieved by exposing it to fishing at an early age. As shown in Table VIII the instantaneous rate of growth between Ages I and II is estimated as 1.99 and between Ages II and III as 0.64. If q were as high as 0.9, then we find by interpolation that the *critical size*, namely, the average size at which instantaneous natural mortality rate equals instantaneous growth rate, comes at about Age II (average size 50 cm). In other words, it is at Age II that a cod year-class reaches its greatest bulk. In the Strait of Georgia, the minimum market size for cod is 18 inches (about 46 cm) and a substantial segment of the catch from some of the grounds consists of two-year-olds. Upward revision of the minimum market size presumably would reduce the potential yield from

a year-class, and this would be of advantage only if it were certain that the spawning stock had been reduced to a size which jeopardizes maximum production of recruits.

It is to be expected also that, in consequence of the high natural mortality rate (short life span), annual fishing success would depend heavily on the numerical strength of incoming year-classes and, therefore, would be relatively unstable. This is indeed apparent in the cod fishery along the Canadian coast—and the northern Hecate Strait fishery serves as a good example. Seasonal (January–April) average catch per hour of fishing by Canadian Class III trawlers (25–49 gross tons), as shown in the following tabulation, has varied substantially during the brief history of fishing. In 1956, catch per hour averaged less than 600 lb, but within the short space of two years it rose to more than 1,500 lb. Corresponding to these changes the total Canadian and United States catch of cod from northern Hecate Strait rose from 3,340,000 lb in 1956 to 11,240,000 lb in 1958.

Year	Average lb/hour	Year	Average lb/hour
1951	1960	1956	585
1952	1000	1957	885
1953	690	1958	1560
1954	940	1959	1105
1955	765	1960	775

Similar instability has been noted in the Nanoose Bay fishery (Strait of Georgia) where average fishing success has varied from as little as 205 lb per hour in 1955 to as high as 710 lb in 1959.

While variations in recruitment probably account in large measure for these annual variations in fishing success, they are not the only factor. It is obvious from discussions with fishermen that cod vary in *availability*¹³, which affects the year-to-year success of fishing. Cod congregate and move in shoals of varying density. Not always will they inhabit bottom which is smooth enough to permit trawling, and of course there may be times when they rise off the bottom and hence escape capture by conventional fishing methods. These variations in availability are difficult to detect and even more difficult to explain. Presumably they are related in some way to the ecological requirements of the cod or of the forage animals which comprise their diet.

As described earlier, the vertical migrations of cod appear, in a general way at least, to be associated with the seasonal cycle of temperature. If cod are adapted to a fairly narrow temperature range, then presumably, they will respond by moving away when confronted with intrusions of water having temperatures much above or below this range. Frequently, fishermen report the sudden disappearance of cod from fishing banks. If these disappearances are of long duration in a fishing season then, obviously, fishing success (average catch/effort) would be an inaccurate reflection of abundance and, as such, would

¹³Availability is here defined as the fraction of the total number of individuals in the fishable size range which, during the fishing season, becomes exposed or vulnerable to the fishing gear.

lead to erroneous estimates of year-class strength or recruitment. This problem would be more serious in the case of short-lived species than in ones which have a relatively long life span in the fishery. Thus, measurement of the strengths of cod year-classes in British Columbia waters is expected to be a difficult task, even if a solution is forthcoming on the more fundamental problem of age determination!

SUMMARY

The Pacific cod is widely distributed in the cooler regions of the North Pacific Ocean and adjoining seas. In waters off the Canadian coast the cod, close to the southern limit of its range, appears throughout the year to occupy depths where the water temperature is between 6° and 9°C—considerably warmer conditions than in regions farther to the north and west.

There is a seasonal vertical migration (deep in winter and shallow in early summer), but the seasonal variation in depth is of only moderate amplitude in comparison with that observed off the coast of the USSR. This difference appears to be a reflection of the difference in amplitude of the seasonal temperature cycle in the two regions.

Estimates of age and growth are dependent entirely on observations of length-frequency modes and on results of tagging, for as yet no satisfactory method has been evolved for determining age of individual fish from scales, otoliths or other hard parts.

Apparently in consequence of the relatively high environmental temperatures off the Canadian coast, the cod has a relatively rapid growth rate during the first two years of life and a short life span. Various estimates of the growth coefficient K range from 0.56 to 0.71 for Strait of Georgia waters and estimates of L_{∞} , the asymptotic length, range from 72.8 to 77.4 cm.

Instantaneous total mortality rates as determined from average size of fish in the catch range from 1.27 to 1.62, while estimates from tagging range from 1.46 to 1.77. These are likely to err on the high side. Likewise, a single estimate of 1.39 for instantaneous natural mortality rate is probably too high, but there is good reason to believe that death from natural causes features heavily in the total mortality rate and that it may be over 0.9.

Sexual maturity is reached at two to three years of age—several years in advance of cod in colder regions of the Pacific Ocean. It is suggested that because of this early maturity and a relatively short life span, mature fish in a typical spawning stock of Canadian cod may be only half as fecund as those in a typical stock from northwestern Pacific waters.

ACKNOWLEDGMENTS

I am indebted to Dr W. E. Ricker for his assistance in designing the analysis of tag returns and to Dr R. R. Parker, Mr Shoichi Tanaka and Mr D. L. Alverson for their helpful criticisms of the manuscript.

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Two Epidemics of Apparent Kidney Disease in Cultured Pink Salmon (*Oncorhynchus gorbuscha*)^{1,2}

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ABSTRACT

Two epidemics of a severe disease in cultured, juvenile pink salmon (*O. gorbuscha*) are described. The symptomatology of the disease and the morphology of the stained bacteria found in tissue lesions suggest that the fish were affected by "kidney disease". If the presumptive diagnosis is correct, this report is the first record of kidney disease occurring in pink salmon.

INTRODUCTION

THERE HAVE BEEN widely distributed epidemics of so-called "kidney disease", a chronic bacterial infection, in populations of most salmonids, and this insidious disease appears to be on the increase. Kidney disease has been studied extensively and the early literature reviewed by Earp *et al.* (1953), so that the present review will emphasize subsequent work. Common symptoms of the disease in young fish include the presence of macroscopic grey-white lesions, pustules and necrotic areas in and on the major internal organs, particularly the kidney (hence the name "kidney disease"), and in its terminal stages, a general bacteremia. In adult chinook salmon (*O. tshawytscha*) the liver and spleen are the primary sites of infection (Wood and Wallis, 1955). Externally, the infected fish may appear normal, or have small blisters on its sides, or the abdomen may be swollen by the intraperitoneal effusion of fluid resulting from renal damage. There may also be exophthalmos. In addition, petechiae may appear on heavily infected individuals, particularly around the vent and pelvic and pectoral fins (Earp *et al.*, 1953; Wood and Wallis, 1955). In any epidemic the syndromes seldom, if ever, involve all of these symptoms.

Microscopically, the affected areas are found to contain large numbers of Gram-positive diplobacilli, 0.3–0.5 μ by 0.5–1.0 μ , which have been established as the etiological agent (Earp *et al.*, 1953; Ordal and Earp, 1956). The organism is aerobic, non-motile, non-acid fast, non-capsulated and asporogenous and is fastidious in its growth requirements. Ordal and Earp (1956) tentatively identified the diplobacillus as a species of *Corynebacterium* but its taxonomic position is still in doubt.

Histologically, the disease is characterized as a systemic granuloma with the bacteria concentrated both intracellularly and extracellularly in the granulomas (Wood and Yasutake, 1956).

¹Received for publication February 10, 1961.

²Paper No. 3 concerning the physiology and behaviour of salmonid fishes, from the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

The natural mode of transmission of the disease, portal of entry and source of the pathogen are still unknown (Wolf, 1958) but artificial infections in salmon have been caused by feeding naturally contaminated food (Wood and Wallis, 1955). However, trout (*S. fontinalis*) could not be infected in this manner (Snieszko and Griffin, 1955; Wolf and Dunbar, 1959), and there appears to be a complex host-parasite relationship in all salmonids. The disease can occur at a low level over a wide range of water temperatures but often increases explosively as water temperature rise. No completely effective treatment exists although various sulfonamides can retard the spread of the disease (Rucker *et al.*, 1951; Snieszko and Griffin, 1955; Wood and Wallis, 1955).

Rucker *et al.* (1954) stated that "Little opportunity is offered for the study of the possible occurrence of the disease in chum and pink salmon since these species remain in fresh water for only a short period before migration to the sea" (p. 301). Such an opportunity was afforded when we were able to culture numbers of pink salmon for an extensive period, not having suffered the usual loss of the stock due to "pin head" formation and other causes. The purpose of this paper is to report what appears to be the first (presumptive) record of kidney disease in pink salmon.

MATERIALS

The fish were hatched from eggs obtained at the Puntledge and Tsolum Rivers on Vancouver Island, and as soon as the alevins started feeding they were placed in salt water. Flowing water was used to keep the fish active during development. When the fish were about 5 to 8 cm long, they were cultured at a level of one fish to 6 gallon (27 litres), so that they were not crowded.

The diet consisted of a mixture of canned salmon, ground beef liver, dried yeast, Pabulum and salt. During the first month the diet included frozen brine shrimp which were fed to demand 8 times a day.

RESULTS AND DISCUSSION

1959 HATCH, PUNTLEDGE RIVER

Typical syndromes of kidney disease were noted in late September of 1959. Mortality rate remained at 2 to 4% per day during the next two months when the rate jumped briefly to 10 to 15% per day despite treatment with sulfamerazine according to the recommendations of Wolf (1958). The stock was then discarded. The fish had reached a mean fork length of 20 to 25 cm. Water temperatures ranged from 5 to 16°C during the period of culture.

1959 HATCH, TSOLUM RIVER

Typical syndromes of kidney disease reappeared in March, 1960, in this stock but the mortality rate was only 2 to 4% per week. However, in view of the previous failure to treat the disease successfully, it was decided to kill and examine all of the individuals in the hope of gaining some useful data. This was done on

April 14 and some of the results are shown in Table I. The actual incidence of disease was probably higher than recorded because the presence of disease was determined only by the detection of macroscopically visible lesions, although the pathogen may be present in considerable numbers even when there are no visible lesions (Wood and Wallis, 1955). Both sexes appeared equally sensitive to the disease and there was no significant difference ($P>0.5$) between the weights and lengths of healthy or diseased fish of either sex. This might indicate that

TABLE I. Sex and mean lengths and weights of healthy and diseased pink salmon, as distinguished by the absence or presence of visible lesions on major organs. Water temperature was at a peak of 11°C at the time of sampling.

Condition	Number of fish	Sex	Mean length	Standard deviation	Mean weight	Standard deviation
			<i>cm</i>	<i>cm</i>	<i>g</i>	<i>g</i>
No kidney	25	♀	204	17	117	38
disease	26	♂	208	17	122	39
Kidney	16	♀	204	13	118	22
disease	16	♂	209	19	124	37

infected fish continued to feed normally at least during the incipient stages of this slow-developing disease. There were no large increases of peritoneal fluid, therefore, it is unlikely that weight losses in body tissue were masked.

Healthy and diseased fish are shown in Figs. 1 and 2 respectively. Apart from the swelling on the caudal peduncle and the small blisters on the skin, there was no external difference. Most of the other diseased fish showed no external symptoms. Internally, however, diseased fish had marked grey-white lesions and necrotic areas on the liver and spleen but particularly on and in the kidney. Normal and diseased kidneys are shown in Figs. 3 and 4. A few living fish even had cardiac lesions and others were suffering such extensive tissue damage that it is surprising they survived. Translucent false membranes were found sometimes on the heart and spleen (Snieszko and Griffin, 1955). The organs first showing lesions were usually the spleen and liver.

The lesions and necrotic areas were found to contain masses of minute (0.5–0.7 μ by 0.8–1.1 μ) Gram-positive rods, many of which occurred in pairs. Microorganisms from the kidneys of 3 infected fish are shown in Fig. 5. The organisms were non-motile, non-sporeforming, non-acid fast (Ziehl-Neelsen) and non-capsulated (Muir's method). The cells showed little differentiation when treated with Loeffler's methylene blue or Albert's stain.

There are no indications how the pathogen was introduced into the culture or how it was transmitted, but it is doubtful if the organism came from the feed. Nutritional inadequacies of the diet might have made the fish susceptible to infection, but comparable stocks of chum (*O. keta*), coho (*O. kisutch*) and sockeye (*O. nerka*) were fed the same diet, yet only two or three coho died apparently from kidney disease. This suggests that these cultured pink salmon might

have an inherent predisposition to the disease. It has been suggested that the disease might be transmitted *via* infected eggs, "carrier" fish or both (Wolf, 1958) and/or by the salmon poisoning fluke (*Nanophyetus salmincola*) (Earp *et al.*, 1953; Snieszko and Griffin, 1955). The debilitating effects of other parasites might also be responsible for initiating this disease (Wood and Yasutake, 1956).

It is likely that this disease affects natural stocks of all salmon but the consequences are still unknown. The scope of a disease in natural populations, particularly of aquatic creatures, is usually very difficult to assess and might appear quite limited because the victims, our "statistics", are soon removed from view by physical and biological agents.

ACKNOWLEDGMENTS

I would like to thank Dr J. R. Brett for his advice and criticism concerning the manuscript. Dr Brett was also instrumental in designing the facilities necessary for culturing the fish. I am also grateful to Mr D. Pozar for his assistance during part of this work, and particularly for his devotion to the culturing of the fish. My thanks are due to Mr C. Morley for the pictures of the fish.

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FIGS. 1, 2, 3, 4 and 5



FIG. 1. Healthy, cultured, male pink salmon (*O. gorbuscha*).

FIG. 2. Male pink salmon from same culture but probably infected with kidney disease. The dark arrow indicates a subcutaneous swelling which contained milky fluid filled with cellular debris and typical Gram-positive diplobacilli. This type of swelling was not common but was one of the few visible, external symptoms. The light arrow shows a small blister, more frequently appearing on infected fish than the swelling

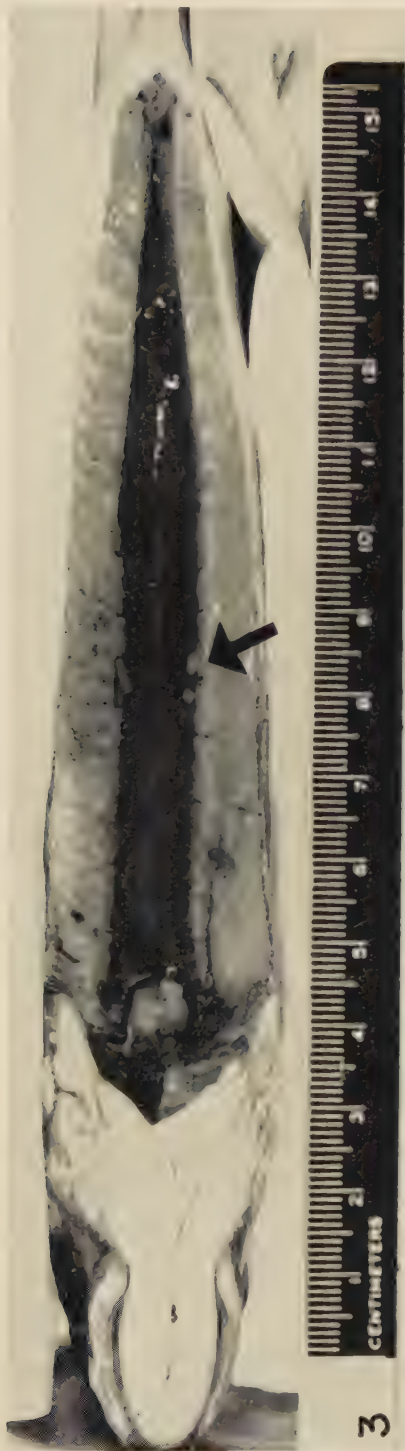


FIG. 3. Healthy, cultured, male pink salmon with kidney exposed. The arrow shows a corpuscle of Stannius

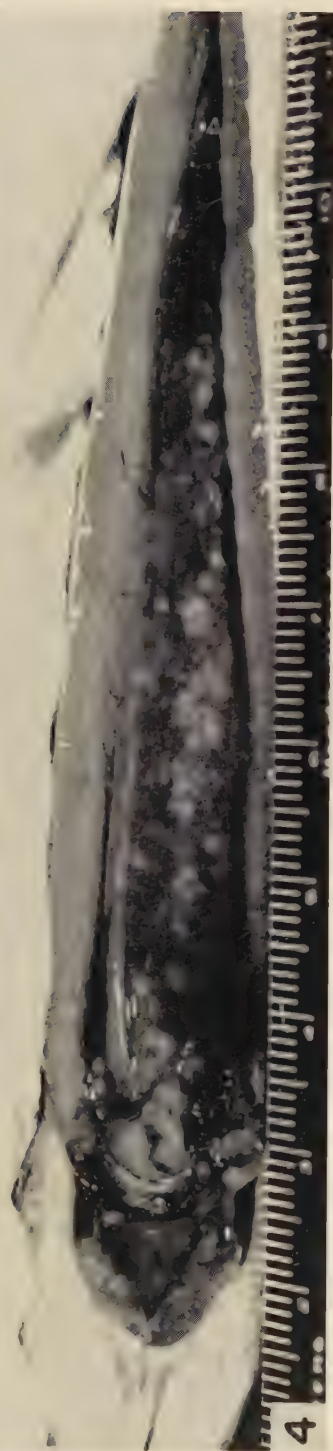


FIG. 4. Diseased, male pink salmon from same culture, kidney exposed to show typical kidney disease lesions which contained masses of Gram-positive diplobacilli.

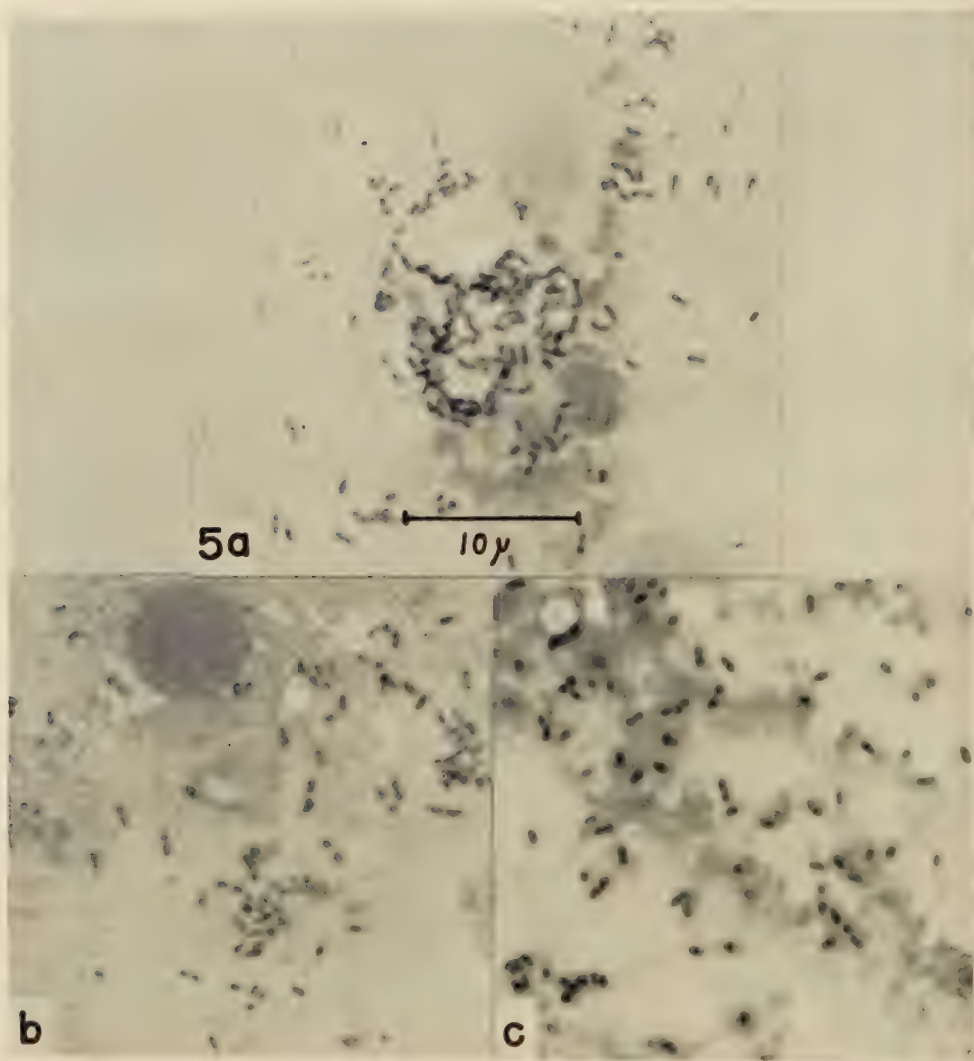


FIG. 5. Gram stains of cells taken from kidney lesions of three diseased pink salmon. Various morphological types are seen in the three fields, a, b and c.

The Annual Oceanographic Cycle at Igloolik in the Canadian Arctic

II. The Phytoplankton¹

"CALANUS" SERIES, No. 17

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ABSTRACT

Phytoplankton populations near Igloolik, northern Foxe Basin, began to increase in late April, and reached their climax in mid-August. The rapid late-August decline of the phytoplankton populations coincided with diminishing light. Diatoms were the main biomass producers in Igloolik and the principal food for the marine fauna. The succession of spring Pennatae and summer Centriceae apparently was caused by light and ice conditions. Taxonomic composition of the Igloolik phytoplankton was influenced by the fast ice and by the shallowness and hydrographic uniformity of the adjacent areas. Descriptions are given of two new species of dinoflagellates, *Gyrodinium arcticum* and *Gymnodinium intercalaris*, and the new coccolithine flagellate *Pontosphaera dilrematolitha*.

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¹Received for publication September 19, 1960.

INTRODUCTION

IGLOOLIK ISLAND has been visited only on rare occasions by arctic expeditions. The *Calanus* expedition occupied a collection station near Igloolik from September 1955 to September 1956 (Fig. 1). The continuity of the hydrographic observa-

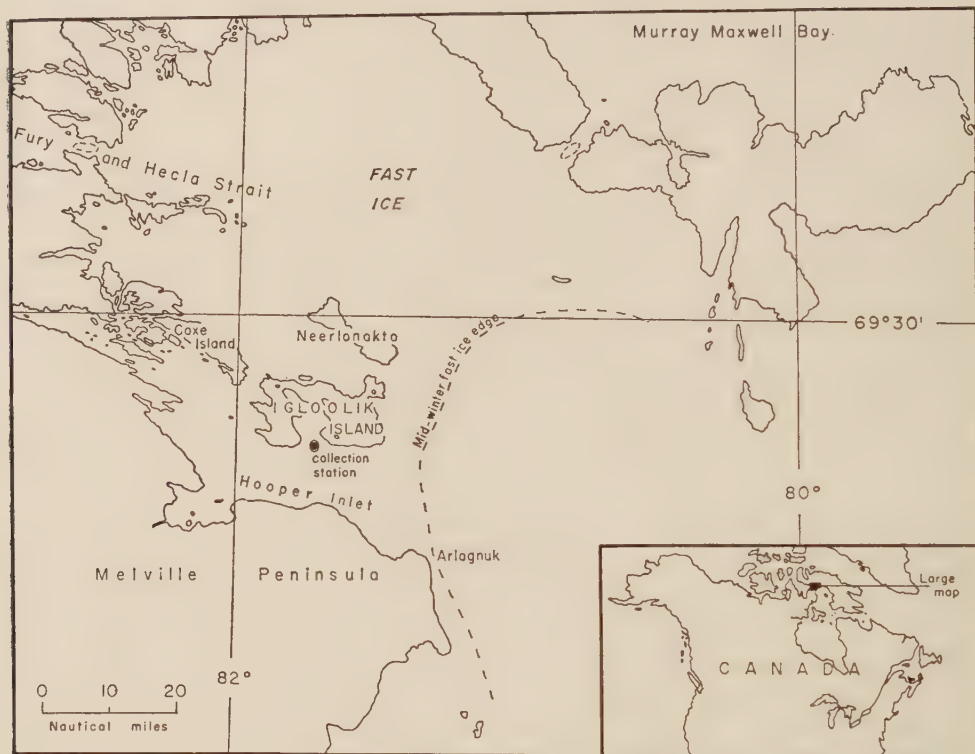


FIG. 1. Northwestern Foxe Basin and the eastern end of Fury and Hecla Strait. The area represented on the large map is shown in the inset.

tions and plankton collections, taken about twice a month, makes this material especially valuable from the oceanographic point of view. Details of sampling procedure have already been described in part I of this series which deals with the zooplankton and physical and chemical data (Grainger, 1959).

METHODS

Quantitative phytoplankton samples collected with a Nansen water-bottle were stored in 170-ml glass bottles with plastic tops, and were later examined with the Utermöhl inverted microscope. Quantitative phytoplankton estimates were made on 25-, 10-, and 5-ml samples after sedimentation in cylinders. Rare organisms, and those difficult to identify, were transferred with a pipette to the

objective glass, then studied under the required magnification with a compound microscope with front phase illumination. It was sometimes convenient, however, to move the dinoflagellates into more suitable positions for identification. This was done by tapping a pencil against the top of the sedimentation cylinder after the quantitative examination of the sample was completed. Both quantitative and vertical net hauls, taken with a net of No. 20 silk, were preserved with neutralized 5% formalin. The efficiency of the taxonomic examination of the vertical net hauls was increased by examination of 1 or 2 cc of net plankton observed later with the inverted microscope. This method seems to be advantageous for studying rare organisms that are often missed when a small number of preparations are studied with the compound microscope. Lugol solutions and methylene blue were used for staining membranes and starch. Javel water was applied for examination of the membrane plates in dinoflagellates. The numerical estimations of plankton were made with objectives 10 $\times$, 25 $\times$, and 40 $\times$. Oculars of 6 $\times$, 8 $\times$, and 12 $\times$ were used according to the size of the organisms under examination.

GENERAL HYDROGRAPHICAL AND ECOLOGICAL FEATURES OF IGLOOLIK

All data on ice, light, temperature, oxygen and phosphates discussed here were obtained from Grainger (1959). Emphasis here will be placed on the biological aspects of the phytoplankton and the relation of the phytoplankton to hydrographical conditions.

LIGHT

Light is a limiting factor for photosynthesis of plankton in arctic, ice-bound regions. Submarine light measurements were not made at Igloolik; however, the duration of the screening effect of ice upon light penetration of the water, lasting from late November until mid-January, is shown in Fig. 2. During this period direct light was completely absent. Direct light lasting 24 hours per day extended from mid-May until the end of July, with nearly equal periods of direct light and darkness occurring in early October and in early March.

TEMPERATURE

Temperature and salinity in northern seas are never limiting factors for plankton as a whole, only for some species (Steemann-Nielsen, 1935). According to Steemann-Nielsen and Hansen (1959), "in the arctic the influence of the low temperature on the rate of photosynthesis is counteracted by a higher concentration of enzymes". The temperature extremes at Igloolik were very narrow (Fig. 2b), between +1.72°C and -1.80°C. The maximum water temperature occurred at the beginning of September, at a time of decline of phytoplankton. The 7-month period of subzero temperature (November-May) was a stagnant one for plants, but one of significant reproductive activity for part of the zooplankton. The first slight increase of phytoplankton populations took place

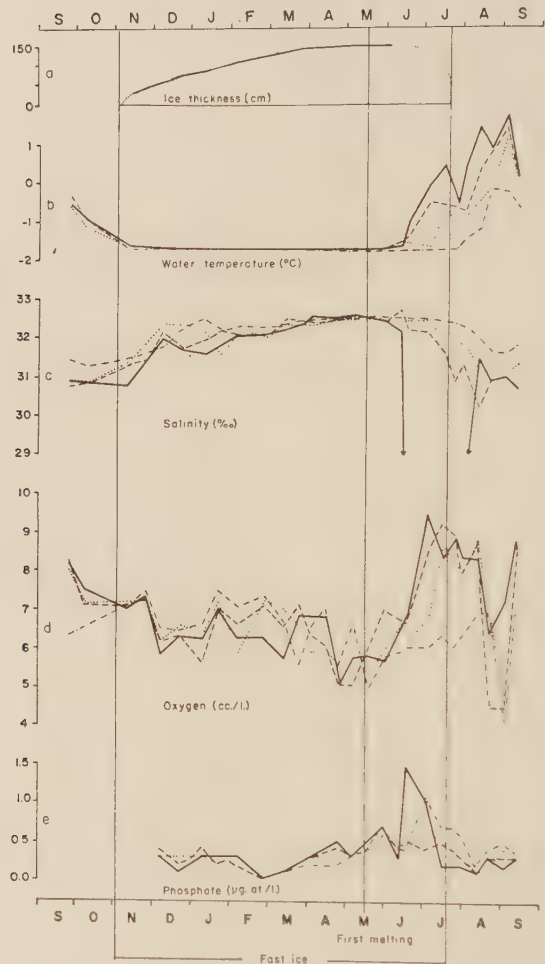


FIG. 2. The annual cycles of (a) ice thickness, (b) water temperature, (c) salinity, (d) dissolved oxygen, and (e) dissolved inorganic phosphate, from September 1955 until September 1956.

Depths are indicated as follows: *surface*, full line; *10m*, broken line; *25m*, dotted line; *50m*, dots and dashes.

after winter when a small rise of temperature (0.5°C) in May was noticed. According to Braarud (1945) small temperature changes in *Chaetoceros* induce microspore formation. Supposedly a similar effect is induced during temperature changes in plankton.

ICE

In the Igloolik area ice thickness increased from November until early May, when it reached 152 cm. Melting began in early May, and continued until mid-July (Fig. 2a).

Ice affects salinity, temperature, light penetration and plankton present in arctic waters. Gran (1904, 1908) found 84 diatom species in the arctic ice previously originated in various ecological niches. The true planktonic forms were more common than freshwater and brackish species. The surface of the arctic ice, melting ponds on the ice, and the under surface of the ice are inhabited by diatoms and flagellates. The flora of these ecological niches varies according to the origin of the ice and its locality. It includes benthic, planktonic, estuarine and freshwater organisms frozen during ice formation.

Regularly stratified ice structure, as observed by the author, was common around Baffin Island in 1956. It developed supposedly in inshore waters, in non-turbulent areas where phytoplankton is abundant. The amorphous, old ice contained benthic organisms when freezing of turbulent water areas took place. As observed by the author during the expedition of the *Labrador* to Foxe Basin in 1956, brown-green layers alternating with colourless ice were formed by trapped plankton diatoms. A piece of ice taken in Lancaster Sound (1956) was melted by the author. Many diatoms became motile again but a great many were plasmolized or dead. Since enormous populations of diatoms are trapped in the arctic ice, ice melting favours their return to the plankton, mostly in June and July. The markedly stratified structure of ice supposedly develops when diatom populations accumulate under the ice surface when freezing takes place. The wider green layers of ice may form when diatoms are numerous and water is calm in late August and September when freezing starts.

A diatom film, collected by the Atlantic Oceanographic Group on March 27, 1957 in the Gulf of St. Lawrence and examined by the author contained 32 species, mostly of planktonic origin. Since they were taken in March and represented large populations it is thought that they had begun to grow early in winter darkness (unpublished data).

The dirty yellow ice of Foxe Basin, typical for this area, shows no special structure, according to Campbell and Collin (1958). It is usually old pack ice which has lost its structure while freezing and refreezing. Four to 8 million tons of ice sediment are formed annually in Foxe Basin, as estimated by Campbell and Collin (1958). During the ice-melting period all nutrients contained in the ice enter the water, stimulating plankton metabolism. Observations by Dr A.W. Mansfield (personal communication) indicate that a prevalent north wind

accelerates the speed of the ice floes carried out from Fury and Hecla Strait. It largely clears the ice from northwest Foxe Basin, as happened in 1956. As a result of southeast winds huge ice fields covered the northern part of Foxe Basin in 1957. Since persistent ice delays the maximum of phytoplankton (Braarud and Hope, 1952), the annual production of diatoms in Foxe Basin is evidently affected.

According to Hutchinson (1957) there is only a small effect of ice-melt water upon growth. The influence of the ice-melt waters under arctic conditions is of particular significance from the biological point of view. Recent research on the phytoplankton productivity in Hudson Bay and in northern Foxe Basin (author's unpublished data), show that low salinities during the ice melting period are associated with poor phytoplankton populations, which increase with higher salinities found in the deeper water layers. In Igloolik the immediate surface layer harboured initial populations of diatoms at a time when no melting had occurred; with a decrease of salinity, plankton populations simultaneously decreased from late May until mid-June, by which time diatom populations were markedly reduced. The gradual increase of the surface populations coincided with rising salinities (Fig. 3) observed between July and September. If occasionally larger diatom populations were found at the surface with low salinity they were presumably brought up from the lower depth where production of phytoplankton was always higher.

SALINITY

Salinity as an ecological factor in the marine phytoplankton was studied by Braarud (1951), who reported variation in the rate of reproduction with varying salinities in Coccolithineae, Cryptomonadineae and Dinoflagellatae. Though specialized salinity requirements were shown for various arctic diatoms (Grøntved and Seidenfaden, 1938), the ecological characterization of species is still far from being settled. The surface phytoplankton is exposed to greater salinity changes than deeper water layers. Microstratigraphy of the surface salinities at Rowley Island (Foxe Basin) made during the *Calanus* expedition of 1957 shows that great salinity changes take place only within 0–2 metres of the surface.

At Igloolik, salinity values varied between 30.70‰ and 31.50‰ at all depths from September 25 until November 10 (Fig. 2c). In early December they rose at all depths, to 32.03‰ at the surface, to 32.12‰ at 10 m and to 32.36‰ at 25 m, and to 32.48‰ at 50 m in early January. Drops in salinity at all depths began in early February and lasted until early May, when they were everywhere between 32.48‰ and 32.59‰. Salinity changes in the deeper layers were slow and presumably did not affect phytoplankton metabolism. Coincident with the first indication of spring melting, the salinity at the surface fell slowly from May 5 until June 13, then rapidly to 27.01‰ on June 19, to 1.68‰ on July 2, and to less than 1.68‰ on July 15. It rose again to 10.41‰ on July 25, to 19.94‰ on August 1, and to 31.56‰ on August 11.



FIG. 3. Histogram showing quantitative features of phytoplankton populations of Igloolik during the entire year at four depths. Counts are given as cells per litre on the logarithmic scale on the left.

OXYGEN

Oxygen distribution at Igloodik is illustrated by Fig. 2d. Oxygen saturation values increased from relatively low values on January 9 to 81.55% at the surface, 82.5% at 10 m, 83.6% at 25 m and 86.5% at 50 m on January 23. This increase could probably be related to introduction of new water masses from the open water area newly illuminated by the sun at that time. Decrease of oxygen took place again on February 7. Increase on February 27 was found not at the surface but at 10 and 50 m. Minor oxygen fluctuations occurred from this time until the end of May, although the size of the diatom population appeared to be sufficient to produce higher oxygen content if light conditions had been more favourable. Dim light under the ice continued until June 19, when a low oxygen level was found in spite of large populations of diatoms. The situation changed on July 2 when supersaturation occurred at 10 m and oxygen saturation percentage reached 102.3%. This could be related to the great phytoplankton populations counted at that depth. The very poor populations at the surface and the relatively high oxygen content of 91.0% were presumably caused by vertical mixing. Further vertical extension of the supersaturated oxygen layer was noticed on July 15, when oxygen reached its highest supersaturation value, 110.3% at the surface and 103.7% at 25 m. Although further increase of phytoplankton populations took place on July 25, there was a slight decline in the oxygen content. This was a time when pennate diatoms were still common but were forming cysts. A rise in saturation values took place from the surface to 25 m on August 11, when the climax of the annual production was reached, with the occurrence of the intensively metabolizing *Centriceae*. Rapid decline in oxygen production on August 20, in spite of large diatom populations, is basically explained by the approaching end of the season and the mass production of resting spores. This decline occurred particularly in the water layer from 10 to 50 m, where the oxygen content was reduced from 55.9 to 49.4%. Some changes occurred on September 13, associated with the replacement of water masses richer in phytoplankton than those observed on September 2, and these may be responsible for the rise in oxygen values to supersaturation at the surface and 10 m, and for the subsaturation at 50 m. Probably new water masses containing still greater diatom populations and higher oxygen content entered the collection station.

Since the general form of the oxygen curve is in fact built up from the oxygen cycles of many plankton organisms, the succession of species and physiological activity in this period of the season could be of value for oxygen interpretation. Since I have observed that great diatom populations are often associated with low oxygen values because of reduced photosynthesis during resting spore formation, a list of species is given, showing: (a) a group of species producing resting spores and auxospores; and (b) species in which formation of the resting spores are not observed. (Tables I and II).

TABLE I. Species of diatoms in which formation of resting spores was observed.

<i>Melosira arctica</i>	<i>Chaetoceros laciniosus</i>
<i>M. islandica</i>	<i>Ch. wighami</i>
<i>Melosira</i> sp.	<i>Ch. curvisetus</i>
<i>Thalassiosira nordenskjöldi</i>	<i>Ch. debilis</i>
<i>Th. gravida</i>	<i>Ch. socialis</i>
<i>Th. rotula</i>	<i>Ch. gracilis</i>
<i>Coscinodiscus grani</i>	<i>Chaetoceros</i> sp.
<i>Coscinodiscus</i> sp.	<i>Biddulphia aurita</i>
<i>Coscinodiscus oculis iridis</i>	<i>Fragillaria cylindrus</i>
<i>Rhizosolenia styliformis</i>	<i>Navicula grani</i>
<i>Rh. alata</i>	<i>N. septentrionalis</i>
<i>Chaetoceros teres</i>	<i>Achnantes taeniata</i>
<i>Ch. lorenzianus</i>	<i>Lauderia glacialis</i>
<i>Ch. compressus</i>	<i>Denotula confervacea</i>
<i>Ch. constrictus</i>	<i>Synedra</i> sp.
<i>Ch. affinis</i>	<i>Amphiprora hyperborea</i>

TABLE II. Species of diatoms in which resting spores were not observed.

<i>Coscinosira polychorda</i>	<i>Bacteriosira fragilis</i>
<i>Thalassiosira aestivalis</i>	<i>Navicula</i> sp.
<i>Th. decipiens</i>	<i>Gyrosigma spenceri</i>
<i>Th. subtilis</i>	<i>Pleurosigma</i> sp.
<i>Chaetoceros atlanticus</i>	<i>Nitzschia closterium</i>
<i>Ch. eibeni</i>	<i>N. longissima</i>
<i>Ch. concavicornis</i>	<i>N. seriata</i>
<i>Ch. decipiens</i>	<i>N. pungens</i>
<i>Ch. perpusillus</i>	<i>Navicula pelagica</i>
<i>Eucampia zodiacus</i>	<i>Thalassiothrix longissima</i>
<i>Streptotheca thamensis</i>	

It is useful, for general orientation, to compare oxygen data from other arctic and subarctic regions. Oxygen content around the Faeroes and Iceland (Steemann-Nielsen, 1935) rarely shows supersaturation, as at Igloolik. In Denmark Strait higher oxygen values and frequent supersaturation were observed by Braarud (1935). In Allen Bay conditions similar to Igloolik were found (Apollonio, MS, 1956). Oxygen data in Hudson Bay show variable features at many stations. High oxygen content in Hudson Strait (Campbell and Collin, 1958) suggests that conditions for growth of phytoplankton in that area are more advantageous than at Igloolik.

Formation of auxospores was encountered in only 6 planktonic diatoms and was rarely observed. No noticeable effect would be made by such a small population on the total oxygen content. The production of the resting spores found in 34 common diatoms and in three dinoflagellates is obviously more significant and may affect total oxygen content of phytoplankton during resting spore formation (Table I). The resting spores appeared first at the beginning of

spring, increased in mid-season, and reached their peak in August. Factors inducing encystment are different; some dinoflagellates form cysts soon after ingestion of other organisms (Schiller, 1933). Germination of cysts takes place in *Chaetoceros* immediately if conditions are favourable (Braarud, 1945). Encystment in *Goniaulax* species in plankton and in *Gyrodinium californicum* in culture has to be related to salinity-temperature changes (author's unpublished data).

PHOSPHATES

Both light and nutrient supply control metabolic activities of phytoplankton (Brandt, 1899). When nutrients are exhausted phytoplankton growth becomes inhibited in northern waters (Braarud, 1935, Kreps and Verjbinskaya, 1930). Decrease of phytoplankton populations in the antarctic took place before any depletion of nutrients (Hart, 1934). Riley (1946, 1953) shows close correlation between the amount of phytoplankton and nutrients.

The values for inorganic phosphate at Igloolik (Fig. 2e) ranged from 0.1 to 0.4 $\mu\text{g-at/l}$ during December, January and February. The lowest values, close to zero, were found in late February. The maximum occurred in mid-June and values declined in mid-July, and were related to increased populations of diatoms. The highest values of phosphates were noticed when salinity dropped during the ice-melting period.

STABILITY

The effect of vertical mixing caused by turbulence may be of considerable importance for phytoplankton dynamics (Braarud, 1935; Gran and Braarud, 1935; Riley and Bumpus, 1946). A stable water column generally permits greater phytoplankton growth (Braarud *et al.*, 1953).

At Igloolik, because the maximum depth is only about 50 m, stability seems to have had very little effect, at least upon photosynthesis, since all populations inevitably were suspended within the eutrophic layer. While slight inhibition of photosynthesis may have occurred at the bottom because of slightly reduced light, the entire 50-metre column may for all practical purposes be considered as being within the depth of active photosynthesis.

Horizontal stratification began in May and became gradually more evident during the summer. This had the effect of creating vertical discontinuity in the phytoplankton distribution, resulting in decreased numbers of individuals in the upper layers during the ice-melting period (when the upper layers underwent drastic salinity reductions). Maximum phytoplankton occurrence was between less than 10 and more than 25 m during most of the spring and summer period. Physical changes occurring on September 2, reducing vertical stability, were accompanied by changes in the vertical distribution of the phytoplankton, many of which evidently ceased photosynthetic activity, formed cysts, and sank to the bottom.

SHORT DESCRIPTION OF THE PHYTOPLANKTON CYCLE

The quantitative assessment made with the inverted microscope showed a steady increase of phytoplankton populations starting from late April. After that time the number of species and their populations increased markedly at various depths. The first diatom maximum occurred in mid-July, after which time a considerable decrease was observed. The second peak, associated with the appearance of more species, began in August. The later rapid increase of populations was associated with formation of resting spores in the majority of diatoms. Large populations of diatoms still occurred in September of both 1955 and 1956. The rapid quantitative decline started in October, and the typical winter minimum with its small populations was observed from November until mid-April (Fig. 3).

SEASONAL CHANGES² IN PHYTOPLANKTON IN 1955-1956SEPTEMBER 25²

Phytoplankton populations on September 25, 1955 were still numerous as far as total number of species was concerned. There were 23 diatom, 9 dinoflagellate, 4 coccolithophorid and 5 ciliate species recorded. The upper waters showed oxygen close to saturation, 96.8% at the surface, 97.2% at 10 m. Maximum production was found at the surface represented by 491,040 cells per litre. At 10 m there were 168,860 cells per litre, at 25 m 57,520 cells, and at 50 m 6,575 cells. The day before this collection was made weather was calm with the temperature near freezing. The quantitative decline of phytoplankton in September is not only an effect of grazing by zooplankton, probably mainly copepods as shown by Grainger (1959), but also is a result of grazing by ciliates which have their climax after the phytoplankton maximum (Fig. 3). Great oxygen reduction took place during the time of zooplankton maximum. The limited light supply at the surface finally stopped photosynthesis and the majority of species produced resting spores.

OCTOBER 5

Phytoplankton populations in October showed equal numbers of cells at the surface and at 10 m. They still represented a sufficient bulk of food for zooplankton in the entire column of water, although the total number of cells was nearly 20 times smaller in October than in September. *Chaetoceros* species were still represented. *Ch. affinis*, *Ch. curvisetus*, *Ch. wighamii*, and *E. zodiacus* exhibited their late maxima of 2,800 cells per litre at the surface, 1,620 at 10 m, and 860 at 25 m. *Fragillaria cylindrus* showed continuous vertical distribution starting from 7,880 cells per litre at the surface, gradually decreasing to 3,260 at 50 m. The smaller number of ciliates showed that both plants and herbivorous forms had reached their final low limit before winter rest.

NOVEMBER 11, 25; DECEMBER 7, 22

The autotrophic plankters were reduced strongly after October 5. The water surface froze and ice reached 33 cm thickness in early November. Five species of *Chaetoceros* formed small populations of a few hundred cells per litre, except for *Ch. compressus*, represented by 1,360 cells per litre at 25 m. Tiny holozoic flagellates were found at all depths in populations varying from 5,600 to 560 per litre. A relatively large number of ciliates (4,260 per litre) and copepods at the surface presumably reduced the phytoplankton to its observed minimum. It is thought that when diatom populations become so reduced that they are insufficient as food, the zooplankton is able to change its diet by devouring various ciliates which are still quite numerous at that time. A further drop in plankton populations took place November 25; 12 species observed under the inverted microscope on that date were represented by only a single or a few individuals. Collections

²Copies of tables showing the quantitative occurrence of phytoplankton species on this and the following dates discussed in this section may be obtained from the author.

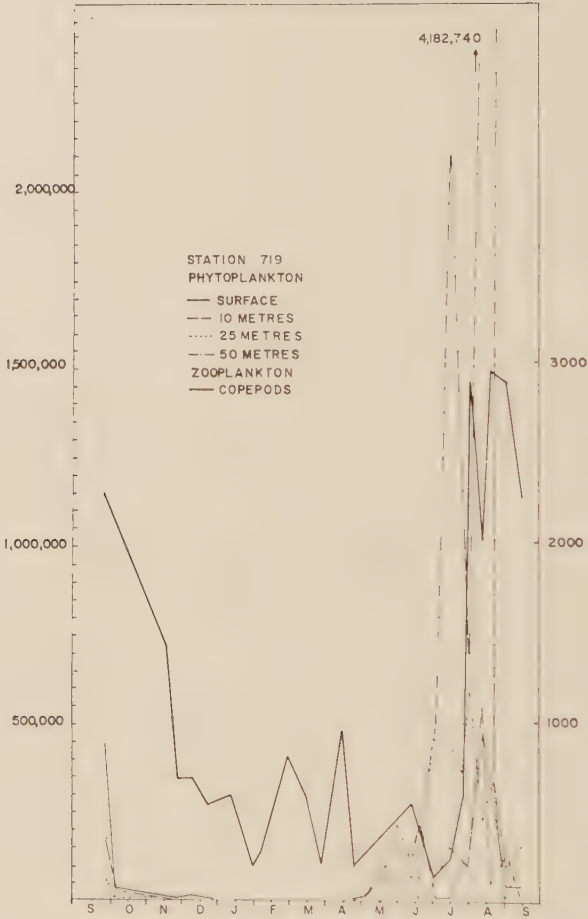


FIG. 4. Phytoplankton populations expressed as number of cells per litre for the four sampled depths, and copepods given as number of individuals per haul.

on December 7 and 22 showed a noticeable increase in diatoms, mainly *Ch. constrictus*, not previously recorded. Presumably this is due to invasion of some allochthonous populations that shifted towards Igloolik. These new populations could be distinguished from the local previously-observed populations by the increased number of *Gymnodinium* sp. and *Warnovia* sp. Observations in December showed further reduction of phytoplankton, especially at the surface and at 10 m. At 25 m there were 17,400 cells per litre of diatoms and flagellated forms. Since the multiplication rate of phytoplankton probably had declined, it is likely that this population was brought in from another area.

JANUARY 9, 23; FEBRUARY 7, 27; MARCH 13, 26

This period showed the typical features of arctic winter. The limiting effects of the ice cover and reduced light supply, associated with low oxygen, drastically reduced the autotrophic plankton to a few individuals per litre. Although poor populations occurred in the sedimentation cylinders (4 diatom species), 14 diatom species and 2 flagellates were found in the net. The lowest point in winter production was reached on April 4 and 14, when only 2 specimens of *Nitzschia closterium* and some holozoic flagellates were recorded. The fluctuation of the total phytoplankton population is shown by the following numbers: January 9, 4,000; January 23, 1,720; February 7, 1,360; February 27, 2,680; March 13, 4,340; March 26, 2,340.

APRIL 4, 14 AND 26

The first increase of diatoms was recorded on April 26, close to the surface under the ice. Arctic diatoms characteristic of melting ice, *Achnantes taeniata* and *Fragillaria cylindrus*, were represented by 1,200 and 1,720 cells per litre. Both populations are considered as initial, after winter minimum. There had been little change in temperature and salinity since April 14. It is supposed that decrease in oxygen percentage from April 14 (79.7% at the surface) to April 26 (59.2% at the surface) is related to the under-ice movement of water. Digby (1953) observed the first diatoms under the ice on April 29 in Scoresby Sound, East Greenland. He concluded that these diatoms could have been brought in by water movements from distant open water areas. My opinion is that the diatoms at Igloolik could have originated as an under-ice film, but could be brought from open water areas as well.

Complete absence of phytoplankton occurred only on April 14.

MAY 5, 19 AND 30

Populations of *Achnantes taeniata* and *Fragillaria cylindrus* increased more than 3 times between April 26 and May 5, providing evidence that spring growth of diatoms proceeded in spite of poor light conditions under the ice. Both diatoms occurred as gradually increasing populations and descended into deeper layers. Small populations of *Chaetoceros compressus* and *Ch. curvisetus* appeared. Small unidentified flagellates occurred between the surface and 25 m in numbers close to the number of diatoms. May 19 showed a still more accentuated phase of increasing autotrophic plants, with the dominant *Ach. taeniata* rapidly developing into populations of 47,960 at the surface, 33,800 at 10 m, 22,400 at 25 m and 1,020 at 50 m. During this period the ice began to melt (Fig. 2). This is also reflected in the salinities of May 5: 32.59‰ at the surface, 32.48‰ at 10 m and 32.50‰ at 25 m. Similar features were found on May 19. After May 5 new species appeared: *Denotula confervacea*, an arctic-neritic form with a population of 21,540 cells per litre at 10 m, and the less abundant *Thalassiosira nordenskjoldi* and *Chaetoceros wighami*. The total number of species included 14 diatoms, 2 dinoflagellates and other minor forms. After mid-May the sun remained above the horizon 24 hours of the day. The rapid increase of the diatom population followed progressive heating of the surface and ice-melting. Though salinity at the surface was only slightly different (32.45‰) from that at 10 m (32.41‰), the surface showed 4 times greater production than deeper layers (Fig. 3). Oxygen at the surface had the relatively low value of 66.3%, despite the fairly large populations of diatoms. It increased to 82.4% at 10 m, then decreased at 25 m where larger populations were found. This presumably indicates more stable waters, which favour phytoplankton metabolism. The maximum May production was reached by *Achnantes taeniata* at 10 m with a population of 174,440 cells per litre, and 66,220 at 25 m.

JUNE 13 AND 19

There was a slight decrease in oxygen at 10 m from May 30 to June 13, and a decrease in surface salinity from 32.45‰ to 32.18‰. More intensive melting began in June and areas of rotting ice appeared over the entire fast ice surface. Plankton production was in an advanced phase, as reflected in the great size of populations and the number of species: 16 diatoms were observed in the inverted microscope and 5 additional ones in the net hauls. Among the flagellated species, some *Pontosphaera*, *Scyphosphaera* and *Lohmannosphaera* were found for the first time in the eastern Canadian arctic.

Observations on June 19 show a further drop in salinity to 27.01‰ at the surface, and relatively smaller populations. This probably occurred because of ice-floes covering wide areas for considerable periods of time. Conditions on June 19 at Igloodik show many similarities to observations made by Braarud (1935) in the pack-ice areas of Denmark Strait in respect to phytoplankton composition and water characteristics. However, this similarity is partly accidental, since environmental conditions in the two areas differ considerably. Braarud's (1935) observations are as follows: when the ice was near by, no large volume of plant production was found, oxygen content was low, the concentration of nutrients was almost the same at the surface as at the lower levels, and salinity was nearly the same at all levels. In all four instances given by Braarud the surface had a smaller phytoplankton crop than the 10-metre layer, where the maximum was found. Though no direct quantitative evaluation of ice influence could be made at Igloodik, it is obvious that ice affects greatly both photosynthetic metabolism and growth. Results of Apollonio (1956) at Allen Bay, Cornwallis Island, show some similarity to those found at Igloodik. Further discussion has to be postponed until more data are available.

JULY 2

There was striking decrease in the size of the population at the surface, as compared with June 19, associated with a drop in salinity to 1.68‰. The fast ice had cleared away from Igloodik Island, and by the middle of July the edge had moved into Hooper Inlet, about half way between southeastern Igloodik Island and Turton Bay. Seventeen diatom species were found with the inverted microscope, including the previously absent *Coscinosira polychorda* and *Navicula vanhoeffeni* which exhibited their initial phase of growth. *Thalassiosira rotula* and *Streptotheca thamensis* were also observed for the first time. *Chaetoceros decipiens*, *Ch. furcellatus*, *Ch. wighami* and *Fragillaria nana* were found in the net hauls. The surface population became reduced to a few individuals per litre. The great populations of *Achnantes taeniata* (267,000), *Fragillaria cylindrus* and *Fr. islandica* (69,000), *Navicula grani* (53,000), *Thalassiosira nordenskjoldi* (34,000) and other less numerous species indicate that the 10-metre depth showed optimal conditions for diatom growth. However, the dominant *Ach. taeniata* had its maximum at 25 m (403,600 cells per litre) and was still represented by 48,280 cells at 50 m. It was the first time that supersaturation of oxygen at 10 m was reached (102.3%). Although very poor populations were recorded at the surface, oxygen was 91.0% of saturation. Oxygen was thought to be produced by metabolically active diatoms before they sank to the lower depths, where plankton populations were much larger than at the surface. In spite of the fairly large number of diatoms, a decrease of oxygen to 79.8% saturation was observed at 25 m, and furthermore it was 71.1% at 50 m. This was a period of intensive increase of pennate diatoms and the appearance of important biomass producers, among which the genus *Thalassiosira* became more important as the season advanced.

JULY 15 AND 25

This was the period of maximum production of the pennate diatoms, of which *Achnantes taeniata* showed 1,440,000 cells per litre at 10 m. Meanwhile *Chaetoceros wighami* and *Ch. socialis* increased at 10 m to great populations of 146,000 and 72,000 cells per litre. Sixteen species of diatoms were found with the inverted microscope, while in the net samples still more occurred, though in small quantities, including *Chaetoceros karianus*, *Ch. septentrionalis*, *Nitzschia pungens*, *N. frigida*, *Fragillaria nana* and *Lauderia glacialis*. Marked increase of species of *Nitzschia* and *Navicula* and *Melosira islandica* indicates that these forms become a potentially strong component of the phytoplankton. This was still more marked in *Thalassiosira nordenskjoldi* and *Th. rotula*,

represented by 153,400 and 135,000 cells per litre found at 10 m. There was further increase in oxygen percentage at 10 m to 110.3%. At 25 m oxygen still showed supersaturation (103.7%), associated with numerically smaller populations and weaker light conditions. On July 23 the ice edge moved almost to Turton Bay, at whose entrance the collection station was situated (Fig. 1), and by the end of July it was inside the bay. The surface water at that time presumably contained much newly melted ice, and its salinity was low (10.41‰). The brackish forms *Chaetoceros socialis*, *Ch. wighami* and *Nitzschia pungens* became more abundant at that time, being better adapted to the low salinities. The general composition of phytoplankton on July 25 showed gradual decline of pennate diatoms, represented by *Achnantes taeniata* and *Fragillaria cylindrus*. Some Centriceae, such as *Chaetoceros wighami* showed their maxima at 10 m, reaching 461,000 cells per litre. The numerical increase in populations of *Denotula confervacea*, *Nitzschia pungens*, *Melosira islandica* and especially of *Thalassiosira* species, also of flagellated organisms, became more noticeable.

AUGUST 1, 11 AND 20

In early August and September 1956 only small patches of fast ice, along with offshore grounded floes, remained around Igloolik. Only occasional ice floes drifted into Hooper Inlet and Turton Bay. On August 1 the total amount of phytoplankton had decreased only insignificantly at all depths, since the previous observation. The taxonomic composition of the diatoms however was changed by the appearance of new species and decrease in the spring forms. The inverted microscope showed 33 species of flagellated groups and ciliates. The net samples showed another 21 species. This was a period of phytoplankton abundance (Fig. 3). In spite of the large autotrophic populations, oxygen values are below saturation. These probably could be interpreted as a result of cloudy weather conditions. Surface diatom production shows only a slight quantitative increase in spite of a considerable salinity increase. This was probably a result of surface water drift, which can not yet be estimated from our observations. Though the largest diatom populations were found at 10 m, those at 25 m were not much smaller. This indicated continuous vertical distribution of phytoplankton. The 10-metre depth showed fairly large maxima of *Chaetoceros furcellatus* of 122,000 cells per litre, 248,000 *Ch. socialis*, 61,000 *N. seriata* and 56,000 *Th. rotula*. This was a period during which the most important diatoms produced resting spores and ceased their metabolic activities, disappearing from the surface.

The climax of the annual production occurred on August 11. Centriceae predominated over the receding pennate forms. The genus *Chaetoceros* was represented by 7 species among which *Ch. socialis* was most numerous and reached its climax of 3,770,000 cells per litre at 10 m. *Ch. wighami* showed a population of 147,000 cells per litre, and *N. pungens* of 124,800 cells per litre. The increase of surface salinity from 19.94‰ on August 1 to 31.56‰ on August 11 is associated with the increase of *Ch. socialis* to 112,000 cells per litre. Similar increases concerned *Nitzschia pungens*, *Ch. furcellatus* and *Ch. wighami*. Dinoflagellates reached their climax and were represented by 9 species, among which the holozoic *Gymnodinium rubrum* exhibited a maximum of 45,000 cells per litre (Fig. 5, 6). It often ingests various diatoms, dinoflagellates and ciliates, and it is thought to constitute an effective grazing element at the time of its maximum. Various Coccolithineae, previously rare or unnoticed, appeared to be abundant (Fig. 8, 9a-n). The supersaturation extending from the surface to 25 m indicated active photosynthesis, decreasing at 50 m on account of reduced light at that level.

Observations made on August 20 showed an evident decline in the number of species and the number of organisms, resulting from decreased light supply, although the number of species was still relatively high. Physiological rest of autotrophs is suggested by lower oxygen values at the surface and within the lower levels.

Observations made on August 26 show a continuing decline of phytoplankton, which could be effectively grazed by the relatively large populations of ciliates and plankton crustaceans and other animals near their annual maximum, as reported by Grainger (1959). The flagellated organisms were mainly represented by *Pontosphaera huxleyi*, with some other species of Coccolithineae found at all depths (Fig. 8).

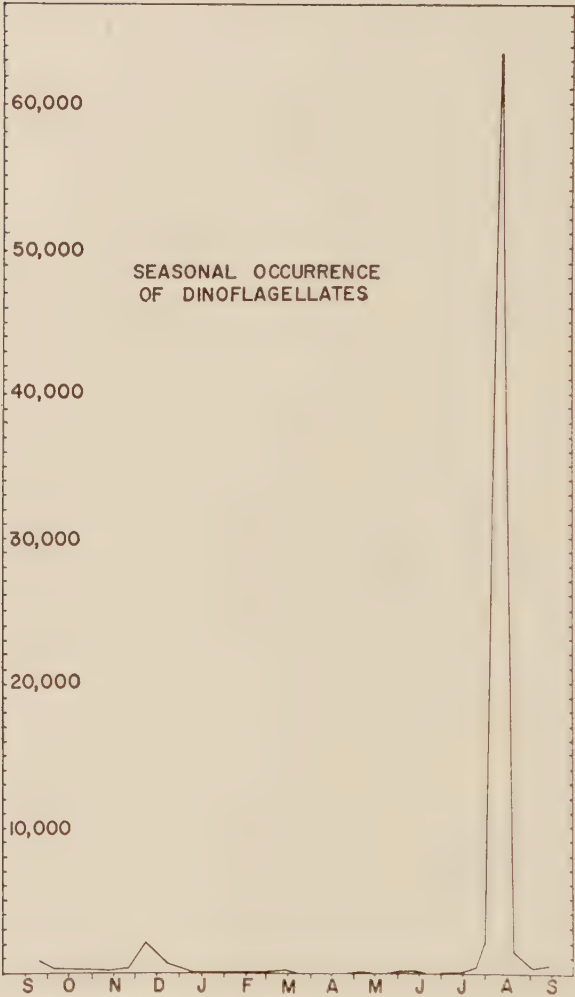


FIG. 5. Seasonal occurrence of dinoflagellates at Igloolik.

DINOFLAGELLATES, FLAGELLATES AND CILIATES - SEASONAL DISTRIBUTION AND MAXIMA

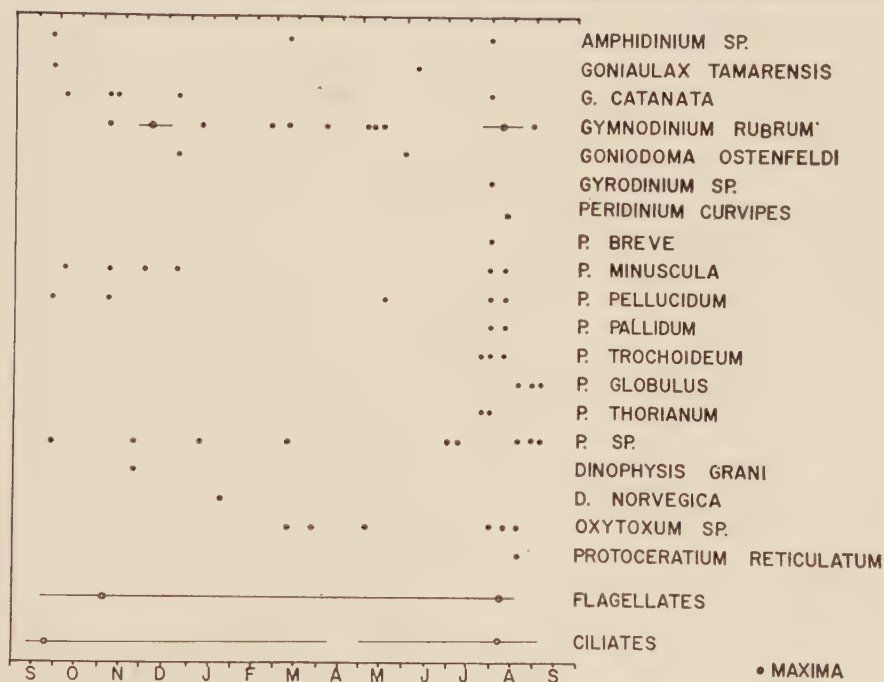


FIG. 6. Seasonal distribution and maxima of dinoflagellates, flagellates and ciliates.

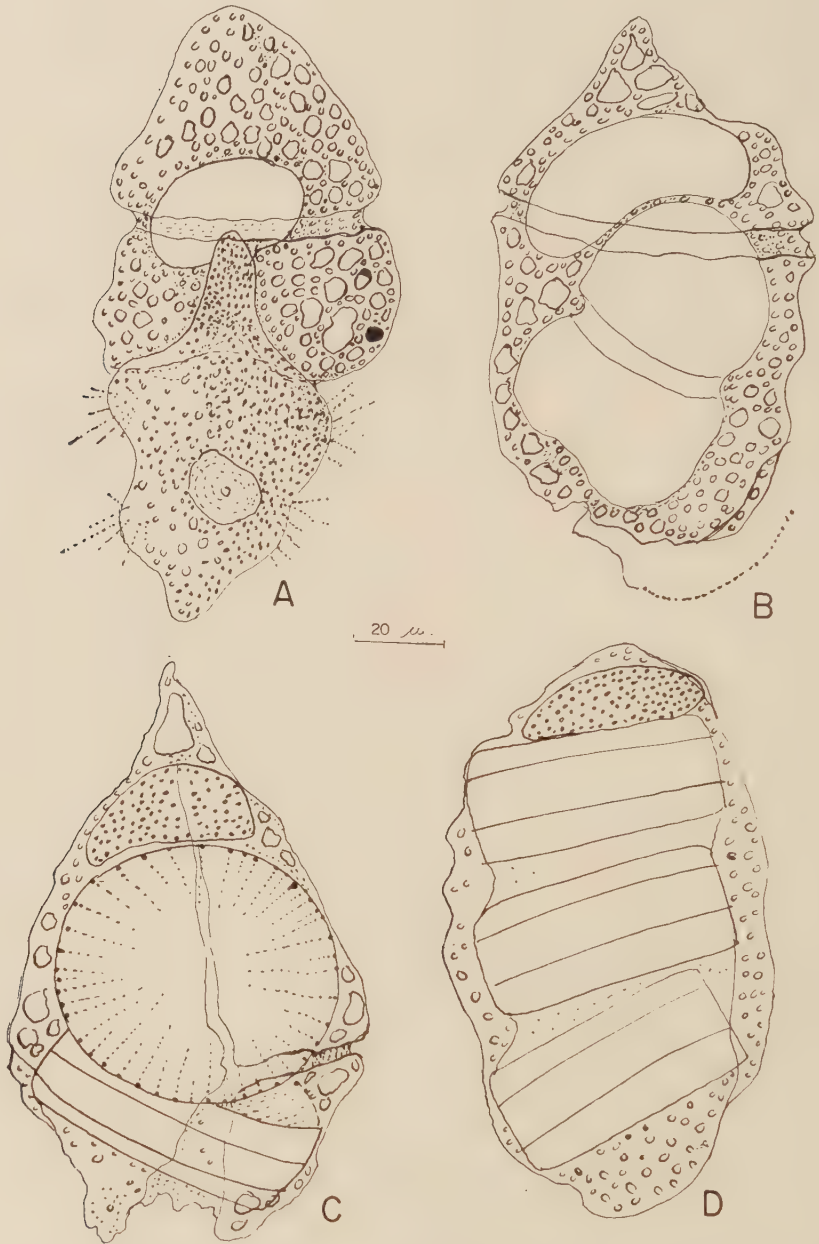


FIG. 7. *Gymnodinium rubrum*. (a) ingesting a ciliate *Strombidium*; (b) containing *Gymnodinium* cell; (c) containing *Thalassiosira rotula*; (d) utterly deformed, containing three cells of *Coscinosira polychorda*, showing nucleus at the apex.

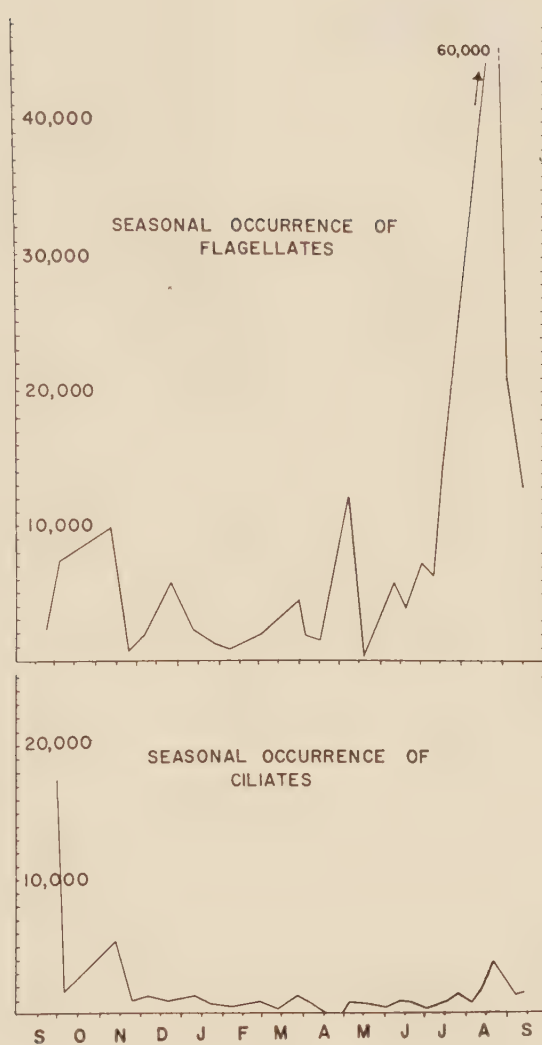


FIG. 8. Seasonal occurrence of flagellates (top), and of ciliates (bottom).

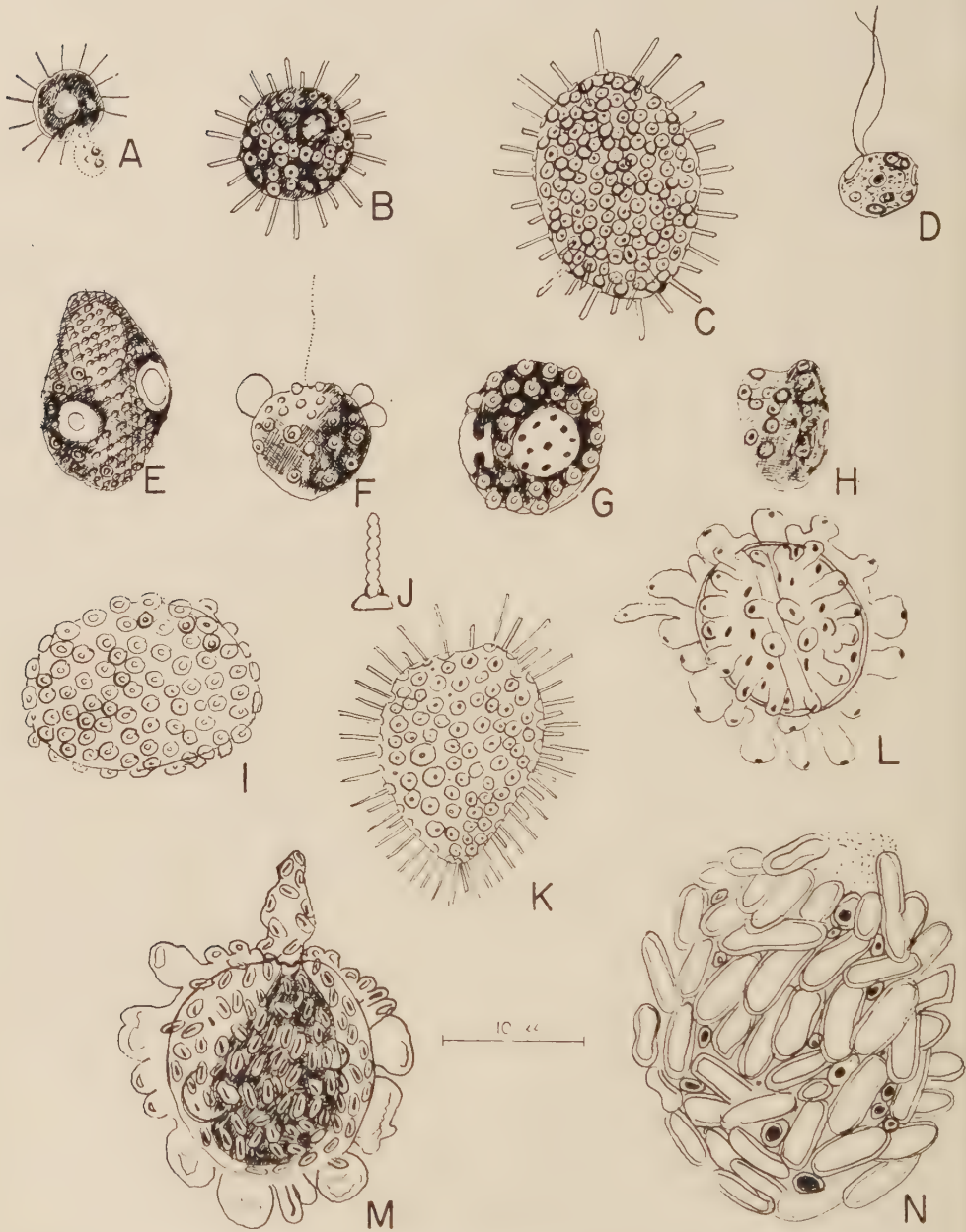


FIG. 9. *Pontosphaera nigra* (a-c), *Pontosphaera huxleyi* (d), *Pontosphaera ditrematolitha* (e-g), *Syracosphaera* sp. (h), *Pontosphaera* sp. (i), *Scyphosphaera* sp. (k), a single coccolith (j), *Lohmannosphaera* sp. (l, m), *Coccolithus pelagicus* (n).

SEPTEMBER 2 AND 13

Autotrophic organisms were represented by 18 species, a great reduction since the late August observation. There seemed to be a definite cessation in metabolic activities except for formation of resting spores, which was quite commonly observed. Vertical oxygen distribution shows subsaturation; the highest value was 93.3%, at the surface, decreasing rapidly to 55.9% at 10 m and 58.3% at 25 m. The water layer at 50 m showed a still lower oxygen content, 49.4% though a relatively large population of over half a million diatoms was found in it.

Observations on September 13 showed an increase of oxygen saturation to 105.2% at the surface and 102.7% at 10 m, while at 25 and 50 m 96.2% and 83.8% were recorded. Presumably new water masses with larger phytoplankton populations replaced the local phytoplankton of September 2. It is not possible, however, to explain this irregularity with certainty, because no data from adjacent areas were taken simultaneously.

VERTICAL DISTRIBUTION OF PHYTOPLANKTON

The vertical distribution of phytoplankton has to be related to various factors such as shape of cells, presence of bristles, and oil or gaseous vacuoles (Gran, 1912; Allen, 1932). Oily discharges from *Coscinodiscus* occurred at the surface of the North Sea (Grøntved, 1952). Experiments were made by the author on preserved *Coscinodiscus* plankton samples. These diatoms which contained large drops of oil gathered in large numbers at the surface of the sedimentation cylinders, while those in which oil was not yet developed covered the bottom of the cylinder. There was also a number of cells suspended in the middle of the cylinder. The floating capacity of diatoms appears to be associated also with the frequency of cell division (Gross and Zeuthen, 1948). Small phytoplankters are better adapted for flotation than are the larger forms (Munk and Riley, 1952). Sinking of phytoplankton in the sea does not necessarily occur in sheltered or calm waters (Grøntved and Steemann-Nielsen, 1957). Igloolik observations indicate that the sinking of diatoms took place when the largest standing crop of plankters was observed to contain resting spores, with membranes of greater specific weight than protoplasm.

Total estimates of the annual mean standing crop at the four depths show striking differences in size of populations (Table III).

TABLE III. Mean annual standing crop of phytoplankton at Igloolik, in number of cells per litre.

Surface	71,038
10 m	357,464
25 m	101,453
50 m	45,043

The surface water, in spite of the high solar illumination, harbours small populations which are exposed to drastic salinity fluctuations. These reach their

lowest values during the ice melting period. The Fisheries Research Board of Canada's *Calanus* expedition in 1957 at Rowley Island showed that brackish water of the lowest salinities formed a layer 2 m deep (unpublished data). Such conditions create a real osmotic barrier for euryhaline plankters from higher salinities below. The maximum phytoplankton production was confined to the 10-metre depth. It was 5 times greater than the production at the remaining depths. The high oxygen values found at 10 m and below in Hebron Fjord in Labrador (Nutt and Coachman, 1956) and those of Igloolik allow one to conclude that the largest autotrophic populations of diatoms generally are found between approximately 5 and 19 m. The mean annual standing crop in Igloolik at 25 m is nearly equal to that at the surface. The mean annual standing crop at 50 m, in spite of the low amount of solar energy, is not much less than the surface crop. This depth in arctic latitudes is usually considered as non-productive, and plankton populations found in it probably do not originate *in situ* but have sunk down from the surface layers.

QUANTITATIVE RELATIONSHIPS

MAIN TAXONOMIC GROUPS

Quantitative relationships among the main taxonomic groups: diatoms, dinoflagellates and ciliates, are shown in Fig. 10. The totals for each group were obtained by adding all plankters of the surface, 10-, 25- and 50-metre samples taken at Igloolik during the 28 station occupations. The largest block of phytoplankton organisms is represented by diatoms, for which the average density was 150,000 cells per litre in the 112 litres of water sampled during the entire season of observation. The main block of the column is divided into a left section representing Centricae, which produced twice as large an "annual crop" as Pennatae, shown on the right side. The extreme quantitative disproportion is apparent when the total of all flagellates, averaging 2,200 cells per litre, is compared with the large number of diatoms. Although dinoflagellates were represented by 32 species, their total "annual crop" was relatively small, averaging 660 individuals per litre. Because the majority of dinoflagellates found in Igloolik were holozoic and only a small fraction were autotrophic most of them may represent grazers, while a small number only are real autotrophic producers of biomass. The smallest block of ciliates, with an average population of 240 individuals per litre, represents real grazers which are of unknown significance in the food chain of plankton. The reader may evaluate briefly the total participation of each group concerned by comparing their "annual standing crops" (Fig. 10).

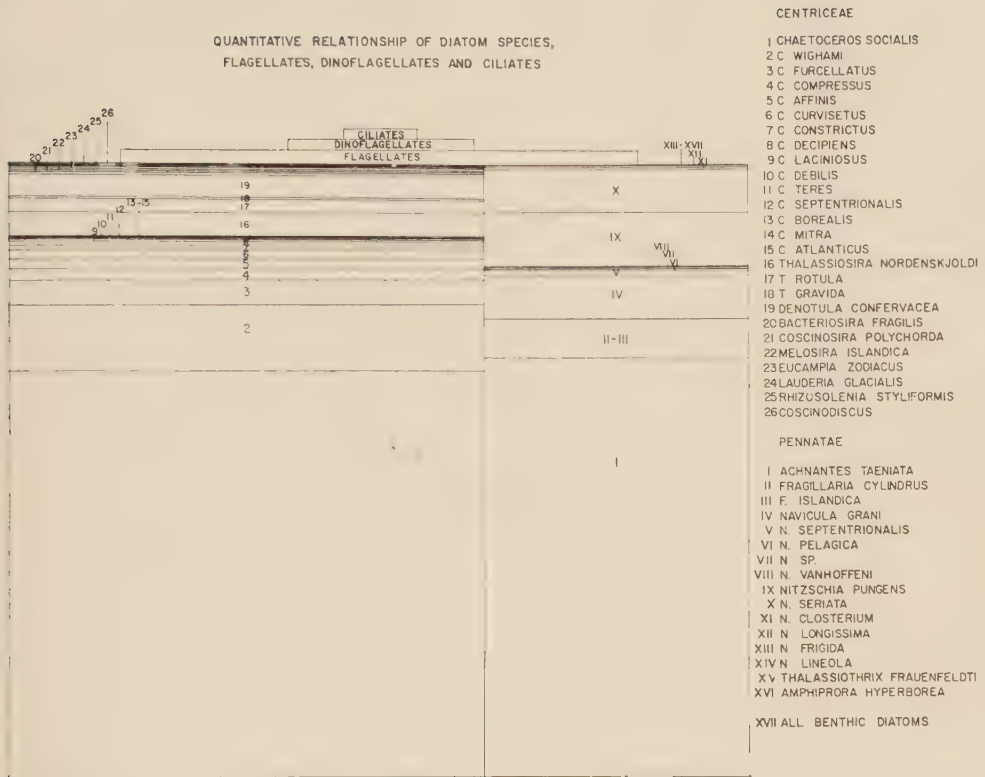


FIG. 10. Quantitative relationship of diatoms, flagellates, dinoflagellates and ciliates. Explanation in text.

ABUNDANCE OF THE VARIOUS SPECIES

The total number of individuals of each species was arranged into 3 groups called major, intermediate and minor, according to frequency of occurrence in the collections. The major group consists of 16 species which are the main biomass producers (Table IVa). The typical arctic diatom element was mainly represented in this group.

The intermediate group consists of 16 species of mixed ecological origin, mostly cosmopolitan and arctic (Table IVb).

The minor group has been divided into those found in the inverted microscope (Table IVc) and those which occurred only in the net hauls (Table IVd). This is in fact the group with the greatest number of species, including 39 diatoms, 30 dinoflagellates, 4 flagellates and 6 Coccolithineae. This group is considered a potential seeding stock, and under favourable conditions may increase in size, thus becoming significant food for zooplankton.

TABLE IV. Major, intermediate and minor groups of phytoplankton species, with their average numbers in cells per litre.

Species	Number	Species	Number
A. MAJOR GROUP			
<i>Chaetoceros socialis</i>	62,685	<i>Nitzschia pungens</i>	4,611
<i>Ch. wighami</i>	10,269	<i>N. seriata</i>	3,640
<i>Ch. furcellatus</i>	3,778	<i>Navicula grani</i>	3,758
<i>Ch. compressus</i>	1,749	<i>Fragillaria islandica</i>	
<i>Ch. subsecundus</i>	1,563	and <i>cylindrus</i>	3,313
<i>Ch. affinis</i>	1,514	<i>Thalassiosira nordenskjöldi</i>	3,514
<i>Ch. decipiens</i>	667	<i>Th. rotula</i>	2,092
<i>Achnantes taeniata</i>	36,432	<i>Denotula confervacea</i>	3,316
B. INTERMEDIATE GROUP			
<i>Chaetoceros laciniosus</i>	394	<i>N. septentrionalis</i>	395
<i>Ch. debilis</i>	162	<i>Navicula</i> sp.	78
<i>Ch. teres</i>	154	<i>Lauderia glacialis</i>	192
<i>Ch. septentrionalis</i>	153	<i>Coscinosira polychorda</i>	286
<i>Bacteriosira fragilis</i>	303	<i>Eucampia zodiacus</i>	264
<i>Melosira islandica</i>	285	<i>Nitzschia closterium</i>	193
<i>Navicula pelagica</i>	209	<i>N. longissima</i>	190
<i>N. vanhoeffeni</i>	0.36	<i>Rhizosolenia styliformis</i>	96
C. MINOR GROUP, FOUND IN THE INVERTED MICROSCOPE			
<i>Chaetoceros borealis</i>	36	<i>Coscinodiscus</i> sp.	11
<i>Chaetoceros atlanticus</i>		<i>Amphiprora hyperborea</i>	4
and <i>Ch. mitra</i>	6	All benthic diatoms	29
<i>Nitzschia frigida</i>	28	<i>Thalassiothrix frauenfeldi</i>	8
<i>N. lineola</i>	23		
D. MINOR GROUP, FOUND ONLY IN THE NET SAMPLES			
<i>Chaetoceros eibeni</i> , <i>Ch. gracilis</i> , <i>Ch. perpusillus</i> , <i>Ch. karianus</i> , <i>Melosira arenaria</i> , <i>M. borrieri</i> , <i>Synedra</i> sp., <i>Coscinodiscus excentricus</i> , <i>Coscinodiscus</i> sp., <i>Fragillaria</i> sp., <i>Pleurosigma</i> sp., <i>Pinnularia</i> sp., <i>Navicula</i> sp., <i>Gyrosigma spenceri</i> , <i>Gyrosigma</i> sp., <i>Nitzschia bilobata</i> , <i>Streptotheca thamensis</i> , <i>Thalassiosira subtilis</i> , <i>Th. condensata</i> , <i>Thalassiosira</i> sp., <i>Cocconeis placentula</i> , <i>Cocconeis</i> sp.			

SOME DYNAMIC FEATURES OF MORE COMMON DIATOM POPULATIONS

Thirteen diatom species were chosen in order to show quantitative fluctuations of their populations in the plankton (Fig. 11-13). Some diatoms, like *Thalassiosira gravida*, *Th. nordenskjöldi*, *Melosira islandica* and *Chaetoceros furcellatus* develop only a single maximum during a vegetative season, this cycle being called unimodal. Species like *Chaetoceros wighami*, *Ch. constrictus* and *Thalassiosira rotula* are called bimodal, since two separate maxima are formed by their populations. The polymodal species show three or more even or uneven maxima.

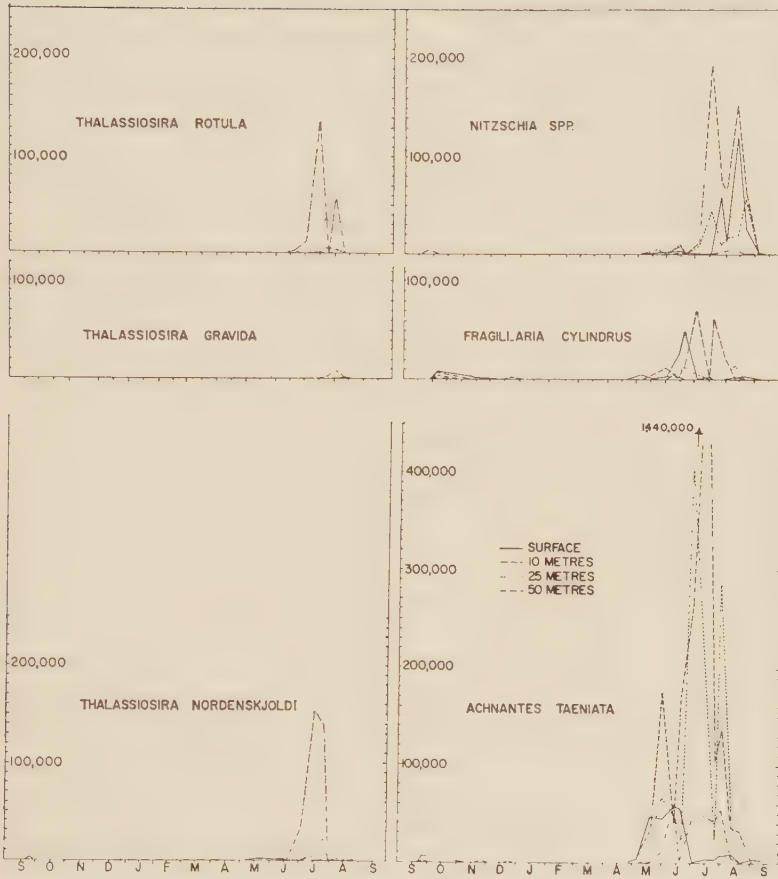


FIG. 11. Quantitative dynamics of the more common diatoms and their annual cycles.

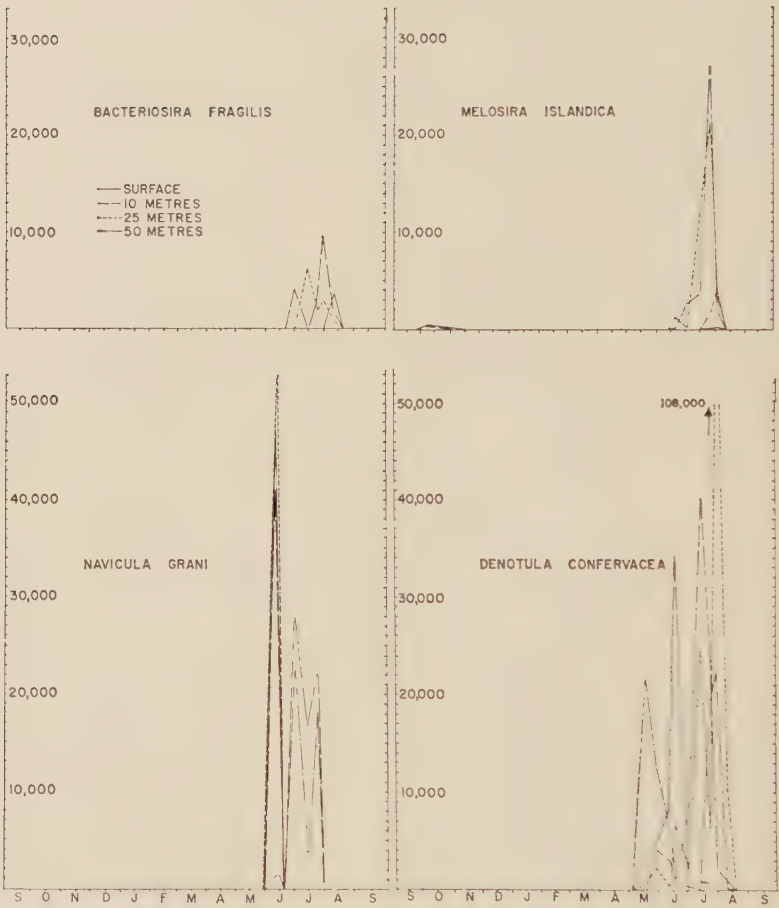


FIG. 12. Quantitative dynamics of the more common diatoms and their annual cycles.

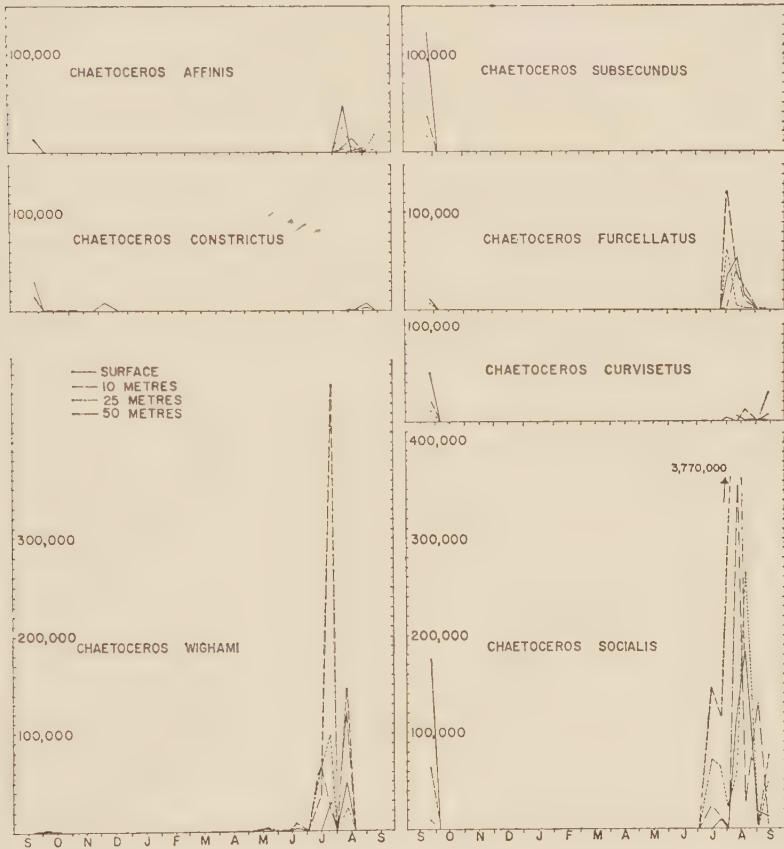


FIG. 13. Quantitative dynamics of the more common diatoms and their annual cycles.

In this group belong *Bacteriosira fragilis*, *Navicula grani*, *Denotula confervacea*, *Fragillaria cylindrus* and *Achnantes taeniata*. Taxonomic identification of diatoms was made using the monographs of Hustedt (1930) and Cupp (1943).

The nature of the quantitative fluctuations in plankton is unexplained. It is supposed that the unimodal type of cycle develops in species where populations are physiologically uniform and show similar features in growth and reproduction. Species exhibiting polymodal curves may consist of physiologically heterogeneous populations, probably differentiated into various physiological groups, which alternate in the sea in sequence with the seasons.

DINOFLAGELLATES

Thirty-two species of dinoflagellates found in Igloolik samples were common only in August and September. The occurrence of most of them in the net hauls was usually restricted to single individuals only, or they were absent from the inverted microscope chambers. To increase the chance of finding rare forms of dinoflagellates, 1 or 2 ml of the plankton sediment were taken with a calibrated pipette and examined with the inverted microscope after filling the sedimentation chambers with water. Such a procedure increases the possibility of finding rare organisms by about 150 to 300 times over the use of single ordinary compound microscope preparations. The time-consuming identifications usually make it possible to examine only a few preparations, so the chance of finding rare species with the inverted microscope are very much better than with the ordinary compound microscope. Works by Schiller (1933, 1937), Paulsen (1908, 1949), and Wood (1954) were used for identification of dinoflagellates.

The thecate forms of dinoflagellates were represented by 19 species, forming small populations seldom exceeding 300 cells per litre. Although the athecate forms were represented by 6 species only, the yearly total of cells collected averaged more than 450 cells per litre. The total number of dinoflagellates taken at Igloolik averaged 665 individuals per litre. The largest populations were 45,000 cells per litre at the surface and 17,670 at 10 m, observed on 11 August, consisting mainly of *Gymnodinium rubrum*.

Some Igloolik dinoflagellates were efficient grazers. Among them *G. rubrum* was able to ingest diatoms (*Thalassiosira*, *Coscinosira*), dinoflagellates and protozoans larger than itself (Fig. 7, a-d). Holozoic nutrition was observed on a few occasions in *Peridinium globulus* (Fig. 14). The cosmopolitan group was dominant, while typical arctic species were less abundant. *Peridinium grani*, *P. quarnerense*, *P. pallidum*, *P. pellucidum*, and *P. minuscula* were more common than *P. roseum*, *P. groenlandicum*, *P. thorianum*, *P. breve*, *P. curvipes*, *Dinophysis grani*, *D. norvegica*, *Goniodoma* sp., *Goniaulax tamarensis* and *G. catenata*.

The preponderance of holozoic over autotrophic dinoflagellates in the Igloolik area is interpreted as a common phenomenon in the arctic biotope, where a natural selection is imposed by the long period of darkness and low temperature. Holozoic

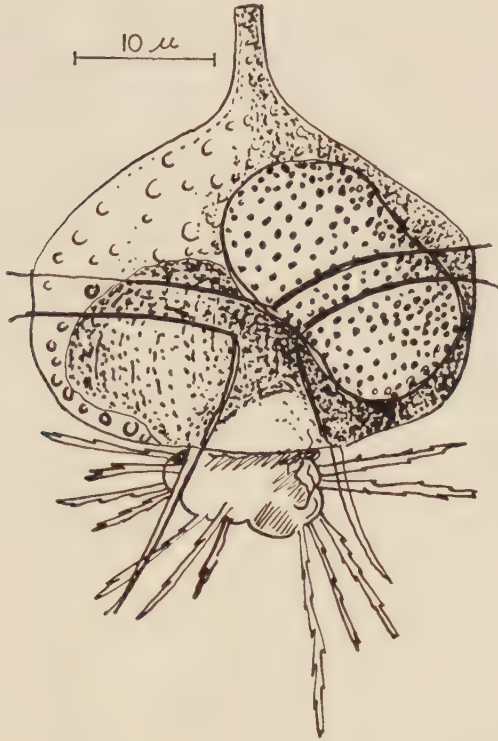


FIG. 14. *Peridinium globulus* ingesting an unidentified flagellate.

plankters appear to be less affected by both these factors, obtaining their energy requirements by phagocytosis, heterotrophy or osmotrophy. Obligatory autotrophs, requiring a light supply as a source of energy, suffer during the long winter.

Intrusion of pelagic *Ceratium arcticum* and *C. longipes*, recorded in the adjacent waters of Foxe Basin evidently did not occur in Igloolik. However, both species are considered as arctic and oceanic (Grøntved and Seidenfaden, 1935), and in the Newfoundland area they are described as essentially cold-water organisms (Frost, 1938). The absence of the large *Peridinium depressum*, found in both cold and warm waters of coastal and pelagic areas, might be explained to some extent in the same way as the absence of *Ceratium* in Igloolik. Probably it is mainly temperature and not salinity which primarily affects the geographical distribution of dinoflagellates, particularly *Ceratium* species (Graham, 1941). This is indicated also by the increase in population density and number of species of dinoflagellates from Igloolik southward towards Hudson Bay. Because dinoflagellates are transported by currents at different times and conditions, they are useful as indicators of the movement of water masses (Wood, 1954). Such

application cannot be practiced without new collection methods however, for dinoflagellates are rare in the arctic. The occurrence of new species, *Gyrodinium arcticum*, *Gymnodinium intercalaris*, *Cenchradius globosum* and *C. spherula* show that the taxonomy of arctic species should be more extensively studied before other problems can be solved.

TAXONOMIC DESCRIPTIONS OF DINOFLAGELLATES

GENUS *Cenchradius* (EHRENBERG)

This genus comprises 4 species incorporated into the family Prorocentraceae (Schiller, 1933). Ehrenberg suggested affinities with Foraminifera. Bütschli considered *Cenchradius* as being associated with warm seas (from Schiller, 1933). The systematic position of the genus is not yet established because the organisms are rare and thus not readily available for study. Both species of *Cenchradius* found at Igloolik appear to be benthic forms occasionally brought into the plankton. The dorso-ventral organization of distinct ventral and dorsal valves occurs only in *C. globosum* (Fig. 15c, d). No intervalvar suture is found in *C. spherula* (Fig. 15b). Both flagellar pores are located at the front of the tube (Fig. 15a, c). The typical membrane pores, as in other Prorocentridae, are found in *C. globosum* (Fig. 15c), while in *C. spherula* parallel warts cover the membrane (Fig. 15c). This form is more elongated than those figured by Ehrenberg. Dimensions of *C. spherula* are $37 \times 27 \mu$, of *C. globosum* $38 \times 20 \mu$. Both species are not previously reported from the arctic. They have been found in the South Pacific (Schiller, 1933).

Gyrodinium arcticum N. SP. (Fig. 16a, b, c)

Body subspherical, asymmetrical and circular in cross section. Sulcus slightly sigmoidal, with a small cavity within the intercingular area, starting on the dorsal surface. Girdle ends prominently displaced. The left end of the girdle usually narrower, laterally oblique, dorsally straight. Sulcus deeply incised, with marked edges. Left lobe of hypocone ending with an acute, subcentrally descending notch and a noticeable margin within the epicone. Fine parallel and horizontal sutures forming distinct square or rectangular plates. Anterior flagellum emerging from the flagellar pore situated at the edge of the upper margin of the girdle. Sulcus deeply incised with marked edges ending as an acute notch where hypocone starts. Membrane surface covered with fine lines running both antapically and horizontally, the latter being less well defined, forming small plates of rectangular and square form. Regularly situated spherical inclusions within the membrane sutures. These inclusions absent within more densely distributed lines in the sulcus. Anterior flagellum starting at the upper edge of the girdle ridge as a flagellar pore. Posterior flagellum emerging at the level where the hypocone notch ends. A hyaline flap of the right hypocone lobe in some specimens covering the flagellar pore. Protoplasm dense, containing small

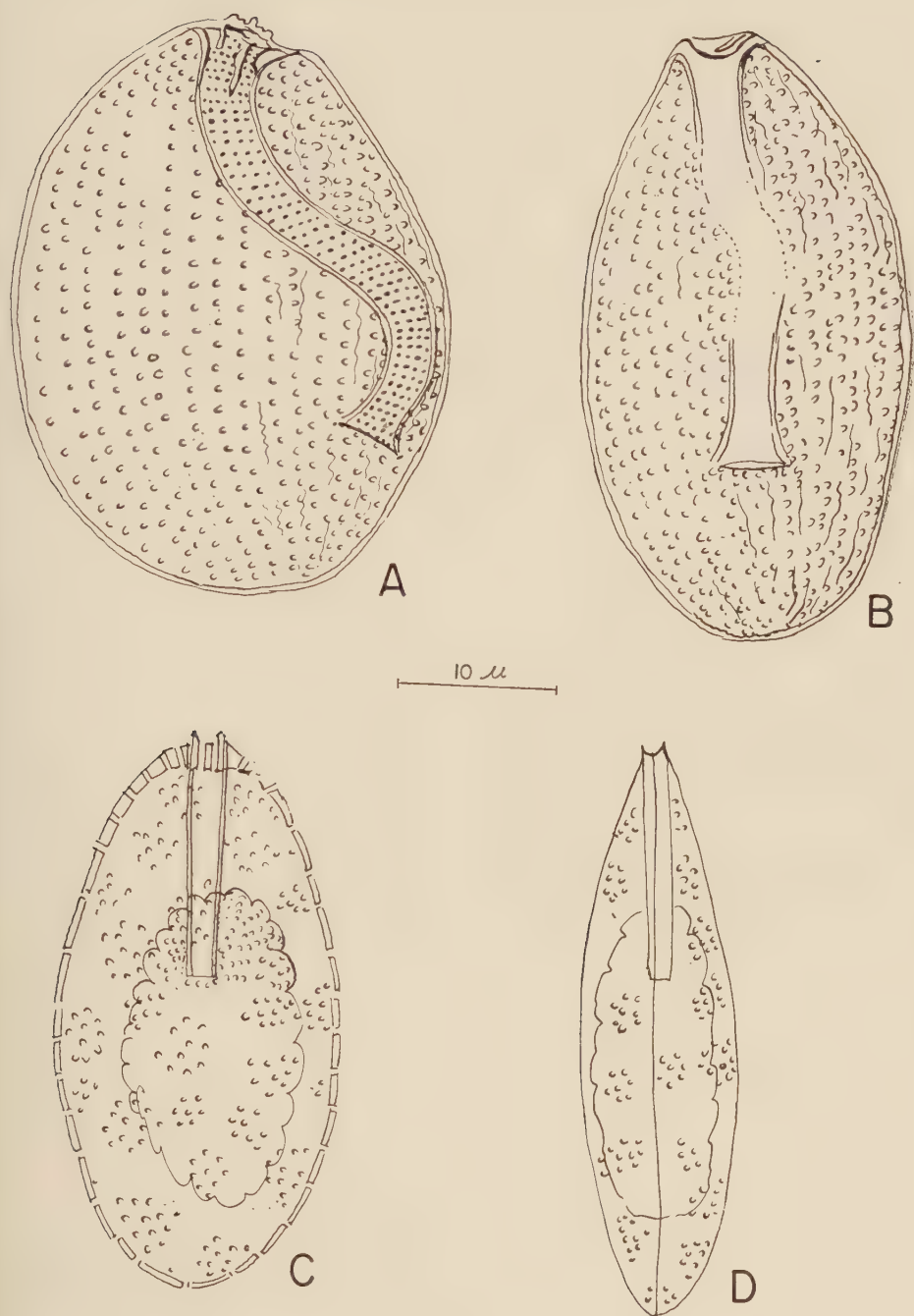


FIG. 15. *Cenchradius spherula*. (a) lateral view; (b) sagittal view. *Cenchradius globosum*. (c) lateral view; (d) sagittal view.

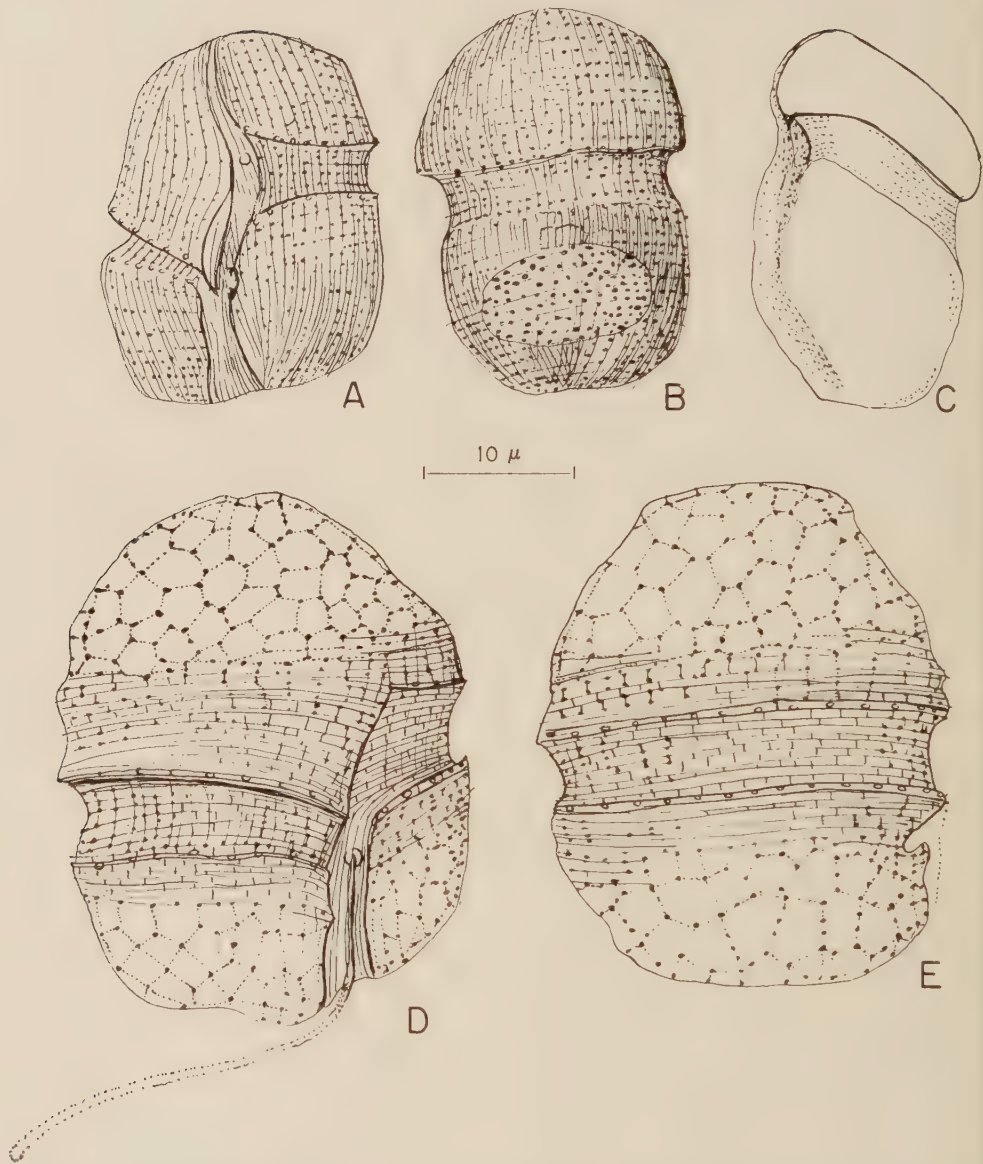


FIG. 16. *Gyrodinium arcticum* n. sp. (a) ventral view; (b) dorsal view; (c) ventro-lateral view. *Gymnodinium intercalaris* n. sp. (d) ventral view; (e) dorsal view.

globular inclusions. Nucleus subspherical with distinguishable chromosomes situated within the hypocone.

Dimensions: length 26–30 μ , breadth 20–28 μ .

Affinities: *Gyrodinium arcticum* appears to be distinct from a group of small and similar species such as *G. hamulus* Kofoid and Swezy, *G. grammaticum* Kofoid and Swezy, *G. incertum* Herdmann and many others insufficiently studied using only low microscope power. All aspects of the morphodynamics of this entire group have to be re-examined in order to establish a proper basis for taxonomic affinities of its members.

Occurrence: Igloolik, August 1956. Net and Utermöhl microscope samples.

***Gymnodinium intercalaris* N. SP.** (Fig. 16d, e)

Body broadly rounded in most cells, subhexagonal in some. Subspherical in cross section with deeply impressed girdle and sulcus. Both ends of the girdle even or slightly displaced. Right section of the girdle three times broader than the left. Sulcus deep but short, ending within a deep edge of the girdle and not appearing within the epicone. Left lobe of epicone larger than the right. Left hypocone lobe twice as large as the right lobe. Epicone ending as an acute, strongly marked edge, clearly separated from the girdle, and protruding over the intercingular area. A small cavity beneath the left edge of the sulcus, visible in dorso-ventral position (Fig. 16e). Posterior flagellum emerging at the level of the left end of the girdle (Fig. 16d). Anterior flagellum not observed. Well marked equatorially located membrane sutures forming a wide belt of "circuli" in which vertical sutures also occur. These structures extending up and down from both sides of the girdle edges. Parallel lines in the sulcus, without horizontal sutures. Both surfaces of epicone and hypocone covered with large polygonal reticulum, containing spherical inclusions. Many suboval chromatophores observed in some cells while others appeared to be holozoic. Small inclusions found in protoplasm. Nucleus not observed.

Dimensions: 34–45 μ .

Affinities: *G. intercalaris* may be easily identified by its "circuli", not observed in other forms. There is some similarity with *G. grammaticum*, but this form is distinct from it and other small *Gymnodinium* already described by Biecheler (1952), Hulburt (1957), and Schiller (1933, 1937).

Occurrence: Igloolik, September, 1956.

COCCOLITHINEAE AND OTHER FLAGELLATES

Great progress in our knowledge of Coccolithineae has been made since the introduction of the electron microscope. The taxonomic nomenclature of some groups has been changed (Braarud and Nordli, 1952; Halldal, 1953; Halldal and Markali, 1954; Braarud, 1955, 1955a; Braarud *et al.*, 1955). The light microscope permits only preliminary observations of the general features of Cocco-

lithineae. The final determination of coccoliths, including taxonomic identification, has to be completed with the electron microscope. In view of this the new taxonomic descriptions of Coccolithineae found in the Igloolik samples are given in a preliminary way only. It is thought that observations made here may be confirmed in the future by the electron microscope, as has happened with diagnoses by Schiller (1930), Lecal-Schlauder (1951), Chatton (1952), Deflandre (1952), and other others.

Coccolithineae are of less importance in the food chain economy of the arctic seas than in the warm seas where they are very abundant (Schiller 1930; Kofoed and Swezy, 1921). The maximum of Coccolithineae in Igloolik was represented by only 60,000 cells per litre, which is in great contrast to the populations of half a million cells per litre found in Hudson Bay (*Calanus* expeditions, 1953-54). There are probably more advantageous temperature conditions in Hudson Bay which particularly favour the development of larger populations of this flagellate.

Pontosphaera huxleyi LOHMANN (Fig. 9d)

Pontosphaera huxleyi was always a dominant component among other species of Coccolithineae. The low degree of calcification of coccoliths found in Igloolik seems to be associated with the low temperature, because such organisms from warmer waters appear to possess well calcified coccoliths.

P. huxleyi was a dominant species among the Coccolithineae. Its maximum appeared late in August, reaching 60,000 cells per litre. Owing to its small size it was identified with difficulty with the inverted microscope. It was more common than any other form of its group at Igloolik and in Hudson Bay. It seems to be common in northern seas (Braarud, 1935; Steemann-Nielsen, 1935).

Pontosphaera nigra SCHILLER (Fig. 9a-c)

Polymorphic form: Populations of this form consisted of spherical and subspherical specimens (Fig. 9a, b). Its spherical coccoliths were usually arranged irregularly, in some individuals densely and in others loosely. Each coccolith was built up of a spherical plate of 0.1 to 1.5 μ diameter from which a fine stalk emerged. The length of the stalks varied from 1.5 to 3.5 μ . The colour of the shell varied from dark brown to dark brown-yellow. The length varied between 3.5 and 24 μ .

Occurrence: July to September, Igloolik.

Pontosphaera ditrematolitha N. SP. (Fig. 9e, g)

Spherical and subspherical cells easily distinguished by their large trematoliths, found mostly as 2 in each cell. Apart from large trematoliths, very small coccoliths also found. These arranged spirally (Fig. 9e) except in the apical area, where absent. The trematoliths of some cells with a large unperforated margin (Fig. 9e), while in some individuals, from 3 to 10 perforations observed. Such trematoliths in side view (Fig. 9g) deeply incised, and both their top and

bottom surfaces joined with a columella. Nucleus apical. Large lateral chromatophore. Single flagellum emerging from the apex.

Dimensions: spherical forms from 9 to 16μ , subspherical forms from 6 to 12μ .

Occurrence: August, Igloolik.

Syracosphaera sp. (Fig. 9h)

Some specimens of *Syracosphaera* sp. were observed with the inverted microscope and were also studied with the standard compound microscope. It was not possible to establish more detailed features, since it was not common enough in the collections. Single minute perforated coccoliths in some specimens covered almost the entire surface of the cell, or else were rare and dispersed. Two flagella of uneven size were seen in some specimens. A single chromatophore and a posterior nucleus occurred.

Dimensions: length from 6.5 to 11μ , breadth from 5 to 9μ .

Most of the cells were badly deformed and not suitable for identification purposes. It was rare in net plankton from August to September.

Pontosphaera sp. (Fig. 9i)

Mostly subspherical, seldom spherical, individuals of this organism were not observed in the motile stage. They were covered with tiny spherical coccoliths irregularly placed. Larger specimens of this form measured between 15 and 22μ . This organism seems to be closely related to *Coccolithophora pelagica*, described also from the English Channel by Lebour (1923). Single individuals occurred rarely in the net plankton in August.

Scyphosphaera sp. (Fig. 9k)

This was distinguished from *Pontosphaera nigra* by its pointed antapex and broad apex. Its coccoliths were of uneven length and heteromorphic, perforated and varying in size. Single coccoliths consisted of a discoid stalk and a stalk with distinct segments. Its calcareous shell was very fragile. Diameter from 10 to 15μ . Its taxonomical position is uncertain. It occurred in August.

Lohmannosphaera sp. (Fig. 9l, m)

These are subspherical cells, easy to distinguish by their apical appendages at the apex of which a usually dark dash-formed perforation is found. A thin fragile membrane of some cells contained two parietal chromatophores (Fig. 9l). In some individuals the cell membrane was colourless, in others, yellow-brown. The length of appendages was greater in larger forms, in which a large apical protuberance usually was formed (Fig. 9m), upon the surface of which dark perforations occurred. *Lohmannosphaera* sp., after treatment with 0.1% HCl, changed its colour to pale yellow and showed small bubbles associated with solution of the calcareous structure.

Dimensions: length of 9 measured specimens was between 15 and 28...

Occurrence: Igloolik, September.

Coccolithus pelagicus (WALLISCH) SCHILLER (Fig. 9n)

Shells were spherical or subspherical with wide apical openings. Coccoliths were large and elongated, sometimes with a distinct septum in the centre, and a narrow margin. In some specimens smaller coccoliths were found close to the apex, while the larger coccoliths were within the antapex. Some were constricted in the middle. Coccoliths were usually placed irregularly on top of each other. Igloolik specimens were similar to those found by Schiller (1930). Halldal (1953) reported it from the Norwegian Sea with a maximum of 16,500 cells per litre; Gaarder (1954) from the Atlantic. Holmes (1956) described it as not abundant from the Labrador Sea.

Dimensions: 32 μ .

Occurrence: Rare in net plankton in August.

CHOANOFLLAGELLATES

Salpingoeca natans Grøntved (Fig. 17a-h)

Two species of choanoflagellates, *Salpingoeca natans* and *Monosiga* sp., were occasionally found in the inverted microscope chambers and net hauls. Both organisms were most common on September 13, 1956, and occurred in small populations of 200 and 500 cells per litre. Thanks to Dr Jul. Grøntved, who kindly sent the author his original sample (No. 6583), taken at 20 m from the southern North Sea, it was possible to compare the Igloolik choanoflagellates with the original specimens. *S. natans* was reported from the Limfjord, Denmark, and from West Greenland. *S. natans* from Igloolik samples appears to be identical with those described from other localities by Dr Grøntved (1952, 1956). However some of the Igloolik individuals were larger. The main difficulty in identifying the Igloolik species was the absence of the outer collar in the majority of flagellates. Only a single collar, showing great morphological variability, was found (Fig. 17a-h). *S. natans* was finally determined when typical individuals with both collars were found (Fig. 17h). The organism is a highly variable one, as far as form and shape of collars is concerned. No stalk appeared in some individuals, which excrete mucus at their antapex, which serves for attachment upon a solid substrate (Fig. 17d). A fine square reticulum of lorica was observed without staining, but was accentuated with methylene blue, which also intensified tiny inclusions in intersections of the sutures. Some protomonades were attached by a small stalk to the inner side of the lorica (Fig. 17h). It was possible to distinguish a cell body from the lorica. A rectangular structure at the base of the outer collar seems to be associated with movements of the collar (Fig. 17h).

A single flagellum slightly longer than the entire length of the lorica with the stalk, emerged from the apex of the protomonade. A well distinguished nucleus was located centrally or subcentrally, containing a large nucleolus.

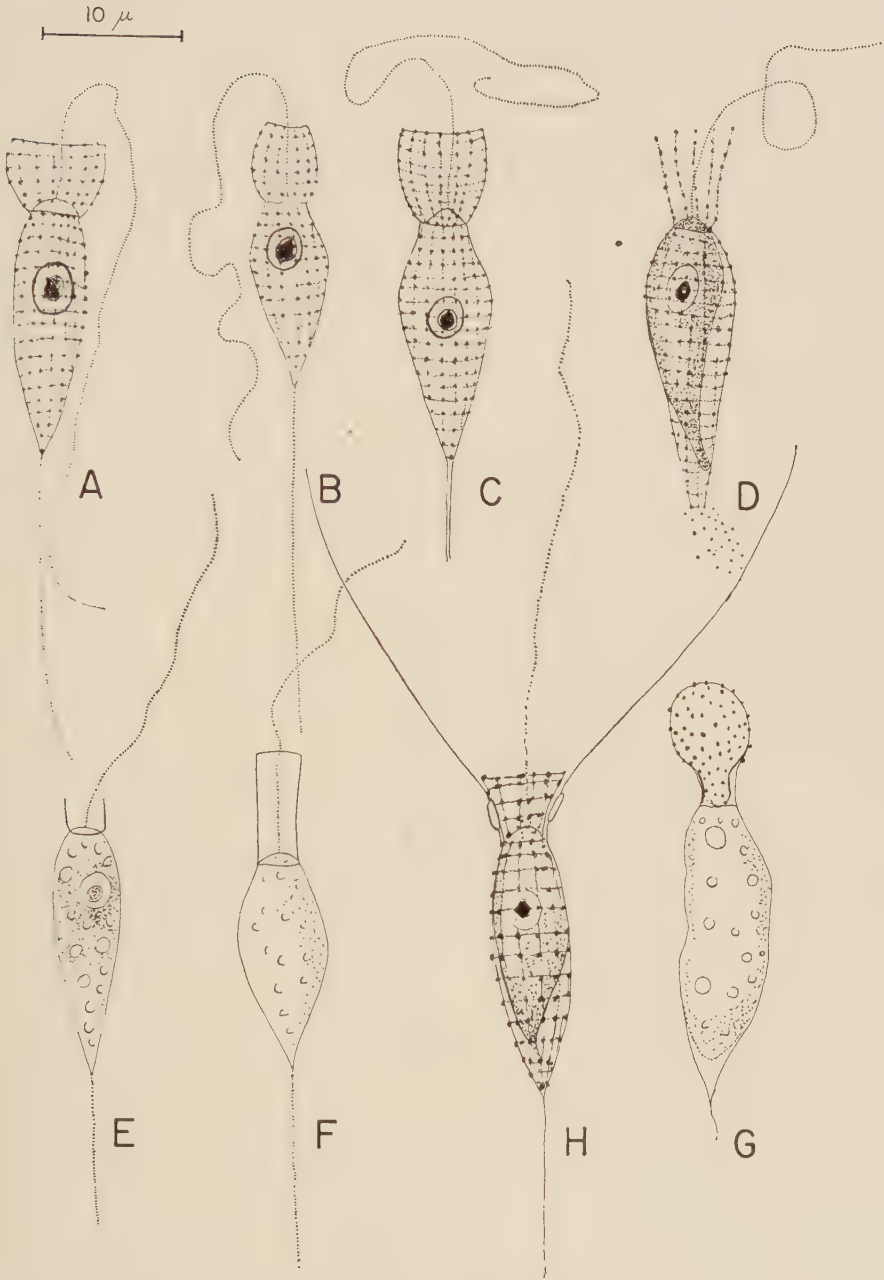


FIG. 17. *Salpingoeca natans*. (a, b) individuals with the long stalks showing fine reticulate structure of the lorica, flagellum and nucleus; (c) individual with short stalk; (d) individual without stalk, the protomonade attached to the wall of the lorica, with some mucus discharged at the antapex; (e, f) individuals with single collar; (h) individual with both outer and inner collar; (g) resting spore formation.

Spherical inclusions in the protoplasm represented reserve materials but were absent in some individuals. Finely diffused brown-green pigment was found in some cells and was most concentrated around the nucleus. It was also observed by the author in some choanoflagellates studied alive (unpublished data). Few individuals were found with the spherical structures attached to the apex, which appears to be a cyst formation. This requires more observations *in vivo*. *S. natans* was associated with a large number of bacteria which, as suggested, it may ingest as food, as observed in other forms.

Occurrence: In August and September more common than in other months.

Monosiga sp. (Fig. 18a-e)

A solitary elongated protomonade was attached to the antapical part of the lorica by a short stalk, and contained a nucleus with a nucleolus. The lorica consisted of three segments partitioned perpendicularly by 10 sutures. Its widely opened collar contained spherical inclusions, stained with methylene blue, within the intersection of the membrane sutures and within the edge of the outer collar. The flagellum was of varying length, usually shorter than the length of the body.

Dimensions: length 26μ , width 19μ (expanded collar).

Occurrence: Rare, mostly found in August.

This species is similar to *Corbicula socialis* (Braarud, 1935), which is colonial, while this form is solitary. Its antapical sutures were well distinguished with front phase illumination. Three segments of the lorica were clearly cut out by the horizontal sutures. Ten antapical sutures divided the lorica into 30 distinct membrane areas, containing fine inclusions, wider within the apex and narrower within the antapex. *Monosiga* sp. appears however to be a distinct species since it shows different morphodynamic features which seem to be absent in the other known species. Final determination was not done because more information is required and its morphological variability should be investigated. It is possible that in some circumstances two collars could be formed in this *Monosiga* as was found in *S. natans*. The possibility of two collars has to be taken into account, since *Diplosiga* sp. (Grøntved, 1956) has two collars and this form seems to be quite similar to the Igloodik organism.

Some details of cell division were observed, showing that both daughter loricas are joined by the edges of their umbrellas, while both protomonades are still joined by a single flagellum (Fig. 18d). The triangular and barrel-like shapes of the loricas in dividing specimens indicated that these are not rigid structures but are able to perform some movement. Some of the protomonades were found separated from the antapical part of the lorica and were freely floating in the plankton (Fig. 18b). *Monosiga* sp. appears to be a non-obligatory plankton organism which can also float freely in plankton or be attached to the surface of diatoms (Fig. 18a).

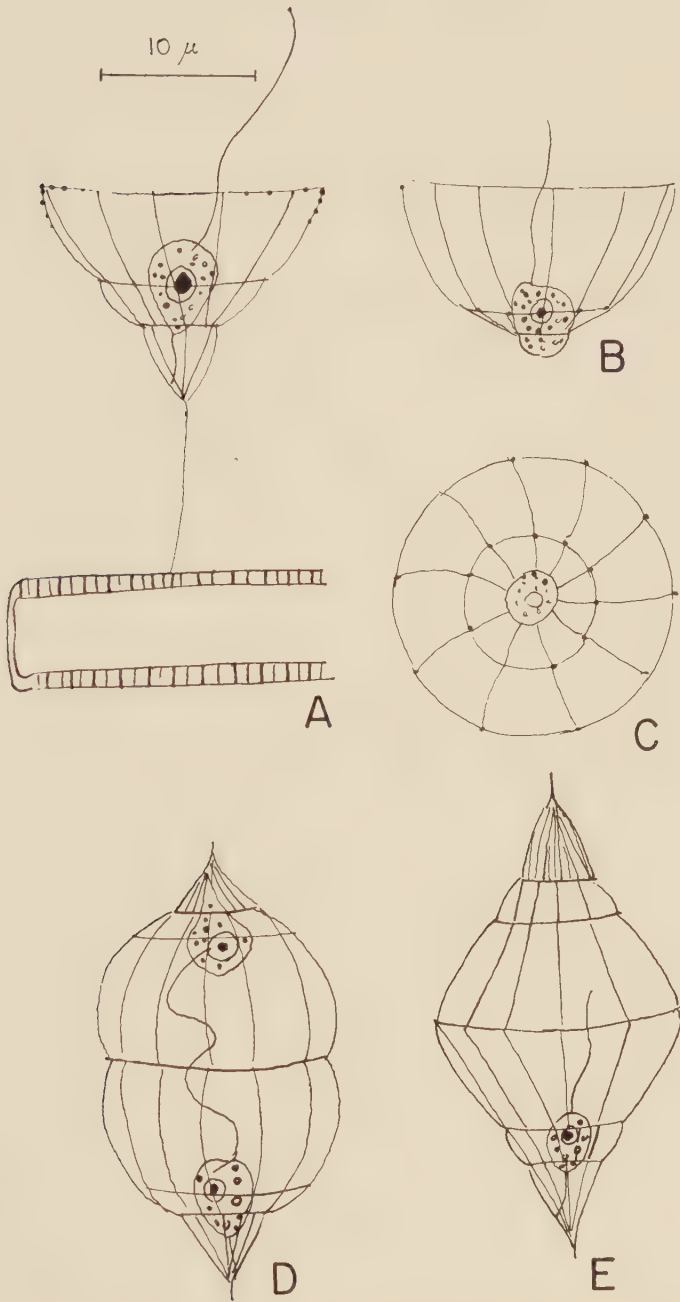


FIG. 18. *Monosiga* sp. (a) an epiphytic individual upon diatom surface; (b) motile individual consisting of the protomonade and upper parts of lorica; (c) observed in front view; (d) two daughter-loricas with a single unseparated flagellum; (e) two daughter-loricas after completed division, of different shape than (d); containing only a single protomonade.

OTHER FLAGELLATES

Some other flagellates found in the Igloolik samples were not abundant enough to be studied in all details. They were identified as *Bodo* sp. and as *Lepocinclis* sp., epiphytic on *Achnantes*. Since *Lepocinclis* Lemmermann (1908) belongs to a freshwater group, it must here be specially adapted physiologically to the marine environment. It was observed in March, when only very poor plankton was observed (Fig. 19).

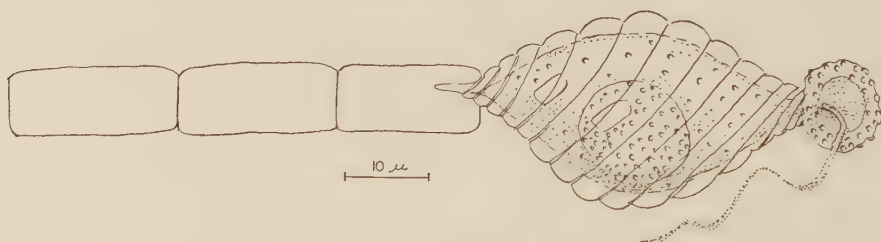


FIG. 19. *Lepocinclis* sp. An epiphytic individual on the membrane of the diatom *Achnantes taeniata*.

CILIATES

Among eleven species of ciliates (identified from Leegaard, 1915) found at Igloolik, *Mesodinium rubrum*, *Lohmanniella oviformis*, and *Laboea conica* were more common than Tintinnidae. Populations of ciliates seldom exceeded a few hundred individuals per litre. The scarcity of species and their small populations seems to be caused by the long period of low temperatures and hydrographic uniformity of the Igloolik shelf. In Hudson Bay (unpublished data) where 27 species were found and greater populations of ciliates occurred, biological conditions appear to be more advantageous. The number of ciliates (28) found in Denmark Strait (Braarud, 1935) is very close to that found in Hudson Bay, while the number (34 species) in Greenland waters collected by Seidenfaden is somewhat higher. It is however not the number of species but the higher total crop per litre which is typical of the higher productivity standard of other geographical areas quoted here. The mean number of ciliates collected at the four depths was 671 individuals per litre. The mean for the surface samples was 135 per litre; there were 148 at 10 m, 268 at 25 m (the maximum), and 120 at 50 m. The seasonal occurrence of ciliates (Fig. 8) shows a late maximum in October and a lower peak in August. When crops of ciliates at Igloolik are compared with populations of single samples from the Norwegian Sea, where 14,200 were found per litre (Halldal, 1953) or with a Labrador Sea sample of 17,200 *Laboea conica* per litre (Holmes, 1956), the low productive level at Igloolik is obvious. Ciliates appear to be effective grazers. Little is known of their individual grazing capacity. They ingest flagellates, diatoms and copepod eggs.

GRAZING

Grazing by herbivorous zooplankton upon phytoplankton is recognized as a significant factor in reducing the size of populations (Steemann-Nielsen, 1935; Braarud, 1935; Fleming, 1939; Riley, 1946, 1953; Riley and Bumpus, 1946; Cushing, 1955). Comparisons of the phytoplankton and zooplankton cycles at Igloolik and Scoresby Sound, Greenland, show that similar general features occur in both areas. It is difficult to make closer estimates since different methods were used in both areas. Data from Igloolik show that the spring increase in phytoplankton and zooplankton occurred almost simultaneously. The increase in phytoplankton and in the number of copepod nauplii (the major herbivores) in April is evident. The commonly described gap between phytoplankton and zooplankton summer maxima does not appear in the Igloolik cycle where the interval, if real at all, does not exceed more than a few days.

The rapid decline of diatoms at Igloolik in the autumn is related to the end of the summer season and increased grazing of great populations of zooplankton. The simplified scheme of grazing in seas usually shows phytoplankton as the main biomass producers and all herbivorous animals as feeders. It is true, but we find that the ciliates and the holozoic flagellates must be also of importance as grazers, and they are not included as a grazing link. The holozoic Gymnodinioideae, which are able to ingest diatoms, Coccolithineae or ciliates (Fig. 7, 14), are significant grazers since they can appear in larger populations per litre than zooplankters. The complexity of grazing has many aspects (Cushing, 1955) which preferably should be studied in the field. In the arctic it is of particular interest to estimate the under-ice film of diatoms found in spring and summer, and probably in winter.

Preliminary investigations were made by the author in order to estimate the intensity of grazing during various seasons as shown by the number of fecal pellets produced by different plankton animals from preserved and unpreserved samples. For such purpose a larger volume of sea water than was used here has to be examined. As the largest number of pellets occurred in August and September, this is the season of most intensive grazing in the arctic. Some of the pellets contained single *Chaetoceros socialis* frustules, while others consisted of empty thecas of *Peridinium* and *Goniaulax*. Both were apparently selectively grazed. The unknown animal whose pellets contained dinoflagellates which were absent in net and quantitative samples, shows great efficiency as a grazer in finding such rare food. The fecal pellets of the omnivorous grazers contained frustules of many diatom species. The number of feeders and size of standing crop of phytoplankton fluctuates according to the seasons, hydrographic conditions, and biodynamics of herbivores. Estimates from Scoresby Sound (Digby, 1953), compared with Igloolik data (Grainger, 1959), show that the size of populations of zooplankton in both areas was similar. The quantitative estimates of the phytoplankton crop show that a hungry season for herbivorous animals began in mid-September and ended in mid-May. This was a period of 8 months, during which fats previously deposited in animal tissues were utilized. It seems possible, however, that many animals may feed on microflora and microfauna of the benthos or turn to cannibalism.

MAIN FEATURES OF THE IGLOOLIK PHYTOPLANKTON

The character of the phytoplankton and its hydrographical background in the Igloolik area cannot be dealt with in isolation, since similar features probably exist within a wide region of coastal Foxe Basin as well as in higher arctic latitudes. The main limiting factor for the marine life at Igloolik is the long duration of fast-ice, which by freezing and melting affects salinity, light penetration and temperature. Shallowness and fast-ice conditions appear to increase the arctic oligotrophy within the wide area where the hydrographical uniformity is caused by a limited water mass exchange with other localities. The phytoplankton populations of the Igloolik station appear to be largely autochthonous because the area concerned is away from the main course of the Fury and Hecla current and mixing is limited. The inflow of this current is directed by the Bouverie Islands towards the southwest side of northernmost Foxe Basin, while its smaller ramification goes through Richards Bay which is very shallow and is covered in some places by grounded ice. This factor minimizes intrusion of Fury and Hecla waters and foreign phytoplankton populations. Allochthonous phytoplankton populations may probably enter within the wide area between Igloolik Island and the Melville Peninsula coast during tidal changes and southeasterly wind activity. The pelagic element is particularly rare, and represented by *Chaetoceros atlanticus*, *Ch. decipiens*, *Ch. lorenzianus* and *Ch. subsecundus*. It seems not to be native to Igloolik, having presumably drifted into the area from the south. The scarcity of warm-water forms like Coccolithineae and dinoflagellates, and the preponderance of arctic and cosmopolitan diatoms, represented by 74 species, indicates ecological features which can be found elsewhere in northern waters. Benthic diatoms were rare, represented by 8 cosmopolitan species, which were noticed more frequently and in larger populations in the Hudson Bay phytoplankton than at Igloolik. The mud-covered bottom of Igloolik does not favour the development of microflora and algae, since only a single rhodophycean, *Phyllophora brodiei*, was taken with the Van Veen bottom sampler. Adjacent Turton Bay appears to be richer and more favourable for both zoobenthos and phytobenthos.

DURATION AND SUCCESSION OF PLANKTON SPECIES

The length of time during which some plankton organisms remain in the floating planktonic phase depends upon the completion of their life cycle. Because the optimum conditions for growth in the arctic are restricted to a few months, the majority of planktonic forms have to complete their cycles in a short period of time. The arctic diatoms soon disappear from the plankton after cyst formation (Gran, 1904). This was observed also at Igloolik, but it was applicable mainly to the brackish neritic diatoms, including melting-ice species.

The pelagic forms like *Chaetoceros atlanticus*, *Ch. borealis* and *Ch. teres* persisted for a much longer period of time in the plankton than those which formed resting spores. The frequency of occurrence of pelagic forms was lower in the sedimentation chambers than in the net samples, in which they appeared continuously even in winter when vertical dispersal affected the number of species in net and sedimentation chambers.

Plankton elements are placed in groups according to the length of time which they spend in suspension in the water (Fig. 6, 20). Those which remained in plankton the entire vegetative season include: *Achnantes taeniata*, *Fragillaria cylindrus*, *Nitzschia seriata* and *Thalassiosira nordenskiöldi*. The others showed a gradually shorter duration in plankton, and include: *Nitzschia closterium*, *Denotula confervacea*, *Nitzschia* sp., *N. grani*, *Chaetoceros decipiens*, *Nitzschia pungens*, *Melosira islandica*, *Lauderia glacialis*, *Eucampia zodiacus*, *Thalassiosira rotula*, *Th. gravida*, *Chaetoceros compressus*, *Ch. affinis*, *Ch. constrictus* and *Navicula pelagica*. The group of shortest duration is represented by *Chaetoceros septentrionalis*, *Ch. debilis* and *Bacteriosira fragilis* (Fig. 21). Diatoms,

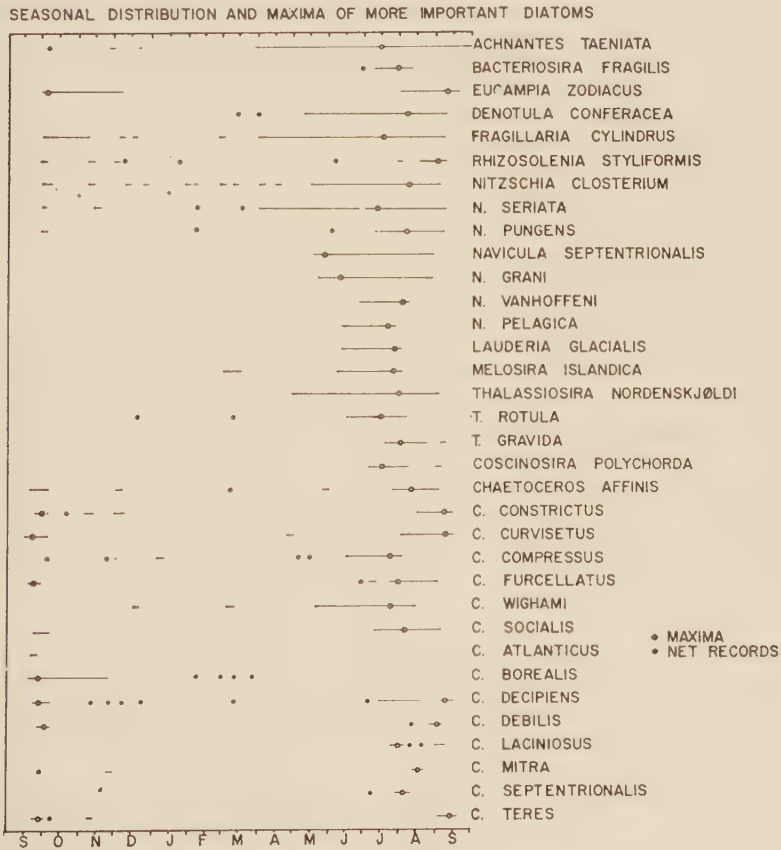


FIG. 20. Seasonal distribution and maxima of the more important diatoms.

as compared with dinoflagellates, flagellates and ciliates, show a distinct dominance.

Seasonal succession in plankton has probably many causes; noticeable in spring are diatoms, and in summer, dinoflagellates. Early spring diatoms were determined as arctic and the latter as boreal. The trend of succession depends upon composition of the initial stock at any time, and it may vary from year to year (Braarud *et al.*, 1953). Apart from the environmental factors, some phytoplankton species can inhibit or stimulate growth of other species by diffusion of metabolites into the water (Rice, 1954). It is thought that diffusion of metabolites may affect not only the size but also the succession of some species. How such biochemical warfare is carried out among different species in the seas is completely obscure. Conover (1956) studied successions of Long Island Sound.

Margalef's (1957) data from Rio Vigo (Mediterranean) show 3 or 4 complete successions of regular pattern, hardly distorted by local irregularities. Winds and tides have hardly any effect upon a pattern of succession. The author is convinced that an arctic type of succession is repeated from year to year, but it could be distorted by turbulence or other factors, as particularly observed at Point Barrow, Alaska (author's unpublished data). The idea of biogeographical regionization and the use of succession for the ecological analysis of plankton and productivity of the arctic (Bogorov, 1958) appears to be useful in its application.

Observations made in different arctic latitudes (Braarud, 1935; Steemann-Nielsen, 1935; Shirshov, 1938; Bogorov, 1938, 1958, 1958a), when contrasted with the Igloolik data, indicate many differences concerning quantitative features of primary production, taxonomic composition and species successions. Davidson's (1931) observations in Hudson Bay on early development of phytoplankton are not sufficient to show annual successions.

Phytoplankton succession in Denmark Strait, begun with flagellates, was continued by *Achnantes-Fragillaria* and *Thalassiosira-Chaetoceros* vegetation, poor populations of *Denotula*, and dinoflagellates (Braarud, 1935). The pennate diatoms appeared in early summer while *Chaetoceros* with dinoflagellates occurred later in the season in the East Greenland current (Steemann-Nielsen, 1935). A succession of *Thalassiosira gravida*, *Fragillaria oceanica*, *Achnantes taeniata* and *Denotula confervacea*, observed by Shirshov (1937; after Bogorov, 1958a) in the arctic seas, was classed as a group of spring species, which were followed by the late-spring species *Chaetoceros furcellatus* and the summer species *Ch. debilis*, *Ch. compressus*, *Ch. diadema*, *Ch. mitra* and *Ch. teres*. Dinoflagellates increased in number as the season advanced. An early spring succession in East Greenland (Digby, 1953) began with *Nitzschia frigida*, *Amphiprora hyperborea*, *Navicula septentrionalis*, *N. grani*, *N. pelagica*, *Fragillaria oceanica*, *Thalassiosira norden-skjöldi* and *Th. gravida*. Because different methods were applied by investigators, the above considerable differences in results have to be expected. Except for flagellates, similarities in the successions were observed between Denmark Strait and Igloolik. All other references indicate in general similar sequences of spring Pennatae, summer Centriceae and dinoflagellates. In the main outlines, succession of the taxonomic groups appears to be repeated within a similar general

pattern established by ecological niches and dynamics of individual species of phytoplankton.

In September 1955 and 1956, Centriceae were represented by 13 species, which obviously dominated the Pennatae. A similar situation occurred in October. The unbalance between Centriceae and Pennatae began in November and continued throughout the winter until the end of April. Initial spring populations under the ice were observed in the late days of April and they started with *Achnantes-Fragillaria* increasing in numbers, associated with initial populations of *Denotula*, *Navicula*, *Nitzschia* and a small number of *Thalassiosira*. Though *Achnantes-Fragillaria* still dominated in early June, the secondary *Denotula-Navicula* grouping became more significant. The decline of "shade" Pennatae took place after July 15, and marked the climax of *Achnantes*. The Centriceae rapidly increased in number of species and size of population. *Chaetoceros* species became most significant until the climax of the Centriceae was reached on August 20. The ribbon-shaped Pennatae constituted a main spring succession, extending into early summer, and became gradually replaced by the summer phase of diatoms, represented by the dominant Centriceae, and late summer dinoflagellates. The comparisons point to the phytoplankton of the waters west of Greenland showing close similarities to Igloolik phytoplankton in the seasonal succession of species (Grøntved and Seidenfaden, 1938). When the ice breaks at Igloolik, a rich plankton, chiefly of *Fragillaria*, is developed. It is replaced later by *Thalassiosira*, and later still by a number of *Chaetoceros* species and the Peridineae. The central Labrador Sea, which is characterized by oceanic species, has a succession distinct from that of Disko Bay, Greenland.

The annual phytoplankton cycle at Igloolik is of the "bimodal" type (Fig. 3). The spring "shade" pennate diatoms exhibited their climax sooner than the summer Centriceae. There was a gap of 28 days which separated the climaxes of Pennatae and Centriceae (Fig. 3). It is sufficient however to classify the annual cycle at Igloolik as the "bimodal" type, in contrast to the "unimodal" type described as typical for the high arctic by Bogorov (1958). Since the net crop, which is recognized as insufficient by the majority of authors, was mainly used for establishing the high arctic type of phytoplankton cycle, the determination of successions of the arctic phytoplankton still remains an open problem in different latitudes. The final solution could be achieved by the use of sedimentation methods and nets allowing quantitative analysis of common and rare species.

BIOLOGICAL SEASONS IN PHYTOPLANKTON OF ARCTIC SEAS

The determination of the biological seasons in the sea has to be based upon principles other than those applied to the higher plants rooted in soil. The seasonal variation in qualitative composition and abundance of organisms permits us to distinguish biological seasons (Bogorov, 1938). Arctic biological winter is characterized by a minimum number of organisms, especially phytoplankton species. Biological spring starts with a slow increase of phytoplankton beneath

the ice. The short biological summer is characterized by an abrupt decrease of autotrophic populations at the end of the season.

Halldal (1953) distinguishes in the Norwegian Sea: winter, from December to March; spring, lasting until June; summer, lasting until September; autumn, from September until October or the beginning of November.

The scheme of biological seasons in the far north made by Bogorov (1958) has been supplemented by the introduction of data from Scoresby Sound, East Greenland (from Digby, 1953) and recent observations from Igloolik (Fig. 21).

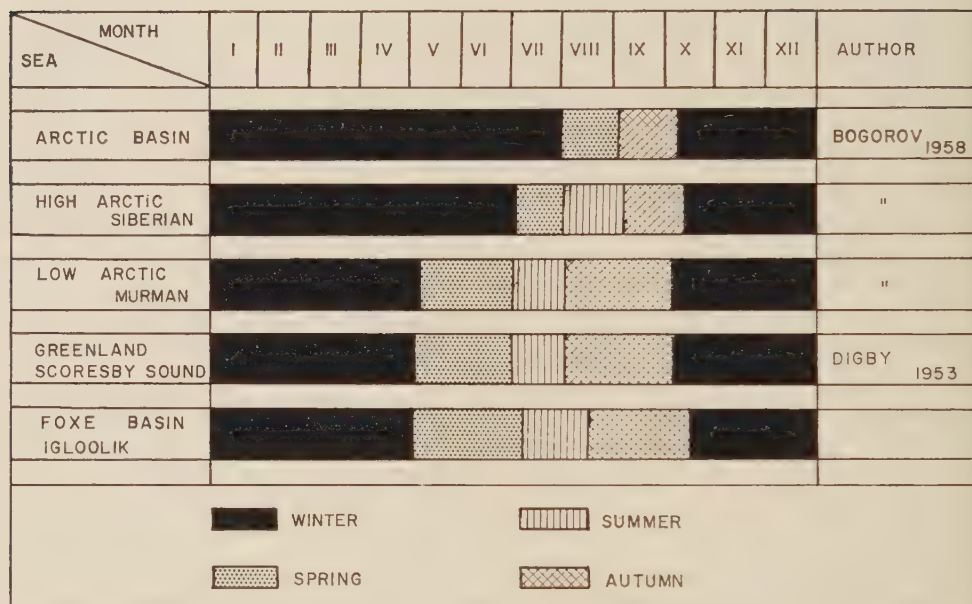


FIG. 21. Duration of the arctic phytoplankton seasons.

The high arctic seas (polar basin and Siberian polar seas) are characterized by a single maximum of phytoplankton. This biological spring corresponds to the calendar months of July and August. In the polar basin the maximum of phytoplankton occurs in August, and in the Siberian Seas in the latter half of July (Shirshov, 1938; after Bogorov, 1958a). The western Barents Sea has two maxima; the biological spring corresponds to the month of May, the biological autumn to August. The more severe winter extends up to 10 months in the arctic basin. Biological spring in the Murman area starts approximately at the same time as in Scoresby Sound or at Igloolik. The duration of biological seasons in the arctic seas (Fig. 21) shows little difference among the regions considered. The beginning of phytoplankton revival after winter has to be related to local ice conditions which vary greatly from year to year from area to area.

Sverdrup (1954; from Marshall, 1958) suggests that phytoplankton production starts in April on the Bear Island Bank and in June in the deeper Atlantic water, and second that as the ice recedes to the northeast over the Central Bank, an outburst of phytoplankton takes place in its wake. In the shallow waters of Igloolik and in Scoresby Sound, Greenland, the spring increase of phytoplankton starts at approximately the same time. It was Ross (1954) who observed that arctic diatoms start to grow even earlier, in March. The under-ice film of pennate diatoms taken in March 1957 in the Gulf of St. Lawrence, by the Atlantic Oceanographic Group, consisted of 32 species that are considered as arctic shade plankters (unpublished data). It is obvious that the plankters had started to grow earlier in the winter darkness. The spring outburst takes place at different times in open and in protected coastal areas (Grøntved and Steemann-Nielsen, 1957). Although the biodynamics of arctic phytoplankton possess their own features, these appear not to be a function of geographical latitudes in the main, as Graham (1941) suggested, but a question of nutrient addition with newly introduced water. We can agree that the intrusion of waters rich in nutrients may invigorate growth of phytoplankton if it takes place during the light optimum required for photosynthesis.

SOME REMARKS ON THE CHARACTER OF THE ARCTIC PHYTOPLANKTON

The pioneer works of Gran (1904, 1908, 1912), Cleve (1873, 1896) and others have been concerned mainly with taxonomic problems of phytoplankton, and its distribution in the arctic. The new approach to the biogeographical divisions of phytoplankton has been applied by Braarud *et al.* (1953). The available data of Polunin (1934), Grøntved and Seidenfaden (1938) and Ross (1954) bring many facts to light on the geographical distribution of phytoplankton species.

The arctic biotope is best characterized by the presence of ice and its ice microflora. It is obvious that the arctic ice flora can flourish in subarctic waters, where they can persist for a rather long period of time. No distinction between the arctic and subarctic can be made, as yet, on the basis of phytoplankton distribution.

Data available (unpublished data) indicate that the biogeographical distribution of phytoplankton is not a function of temperature only, but of both temperature and light. It is obvious that a group of diatoms forming a large population under the ice may be considered as a "shade" flora, if it is absent where there is no ice, and therefore typical for the arctic environment. Steemann-Nielsen, from his results of Carbon-14 investigations, concluded that light adaptation of phytoplankton is possible, and Steemann-Nielsen and Hansen (1959) concluded that "none of the many plankton surveys from the arctic has shown any indication of the occurrence of a special 'shade' flora". Large

populations of the flagellated organisms found by Rodhe (1955) beneath the ice of a subarctic lake in Sweden in winter must be considered as a "shade" group. Obviously the ribbon-shaped Pennate diatoms found in April beneath the Igloolik ice were grown under ice impenetrable by light, and must too be classed as a "shade" flora.

It is however possible that there is a considerable light adaptability in arctic diatoms which can flourish in almost any light condition found in the arctic, if nutrients are available. The Centriceae diatoms, most abundant during the open water period, where maximum light is available, may be contrasted with the "shade" Pennatae as a "sun" flora. Possibly the succession of the spring "shade" by the summer "sun" group of diatoms has been induced by different physiological requirements in each group. Diatoms are dominant in the dark arctic environment, because they can tolerate long periods of darkness at low temperature.

The size of the phytoplankton populations and their taxonomic composition is a good ecological indicator for classification of waters in different latitudes. The total list of phytoplankters from Igloolik includes 121, in the slightly warmer Hudson Bay it is 235 (unpublished data). In the region of Point Barrow, Alaska, the number of species was still higher, 286 (unpublished data). The number of dinoflagellates reflects particularly well what is said above. They increased from 32 species found in Igloolik to 91 found in Hudson Bay (unpublished data). The increase of flagellated groups from north to south is related to the weakening grip of severe arctic conditions, to the increase in temperature and in solar radiation found towards the south. Not nutrients but temperature mainly favours developments of dinoflagellates (Gran, 1912; Graham, 1941; Wood, 1954). Preponderance of flagellates over diatoms in the southern latitudes is exemplified well by the plankton list of Rampi (1945) from San Remo, Monaco, where 350 species occurred, 245 of them dinoflagellates. I believe therefore, that the character of the ecological conditions of ocean waters could also be determined from the biological balance shown by the quantitative relationship of diatoms and flagellated organisms.

SUMMARY

1. A collection station was situated at 69° 20.5' N, 81° 43.5' W on the coastal shelf of the northern part of Foxe Basin. This area was covered for about 9 months by fast ice, a limiting factor for phytoplankton life.
2. Sea water samples for phytoplankton, studied by the sedimentation method, were collected about twice a month from September 1955 to September 1956, at the surface, 10, 25 and 50 metres depth. Vertical net hauls for taxonomic examination were also taken. Interpretation of temperature, salinity, oxygen and phosphates was also made.
3. The predominance of low temperatures (within a range of 3°C), and ice and light conditions influence the taxonomic composition of the phytoplankton

and the size of its populations. The absence of various taxonomic elements and some uniformity of general phytoplankton features seems to be related also to a small degree of communication by currents with other adjacent areas.

4. The vertical occurrence of phytoplankton at Igloolik was greatly differentiated in the course of the season. Phytoplankton populations at the surface from April 26 to May 19 were nearly equal to those found at 10 m. They became slightly higher in June, and were markedly lower in July, then increased when the effect of melting ice and low salinities had diminished.
5. Although maximum phytoplankton production was at 10 m, the trophogenic layer in the ice-melting period presumably started from about 2 metres depth and extended down to about 15 m. Below 10 m phytoplankton populations diminished with increasing depth.
6. Four biological seasons were distinguished at Igloolik. *Spring* started in April, with an *Achnantes-Fragillaria* bloom, and lasted until July. It was marked by maxima of the pennate diatoms, succeeded in early summer by the Centriceae. The climax of the Pennatae appeared on July 15, that of the Centriceae on August 11. The latter coincided with maxima of dinoflagellates and Coccolithineae. *Summer* began at approximately the end of July, with increasing populations of Centriceae. September and October represented *autumn*, marked by cessation of metabolic activities. The biological *winter* lasted from November until April.
7. Since the majority of the numerous brackish-neritic diatoms were metabolically passive because of cyst formation, they were often associated with low oxygen content of the water.
8. A taxonomic list of species is given. Three new species, *Gymnodinium intercalaris*, *Gyrodinium arcticum*, and *Pontosphaera ditrematolitha* are described. For the first time two rare and little known species, *Cenchradius spherula* and *C. globosum*, were noticed in the plankton of arctic waters. Nine Coccolithineae, two Choanoflagellates and a few little known flagellates were also studied in detail.
9. The quantitative dynamics of phytoplankton populations and their vertical occurrence were contrasted with those of other geographical latitudes.
10. The general taxonomic composition of the Igloolik phytoplankton seems to be greatly influenced by the severe ice conditions associated with poor light supply, hydrographical uniformity and shallowness of the area.
11. The holozoic dinoflagellates were dominant in the Igloolik samples, while brown autotrophic species formed only small populations. The strong-membrane Peridineae and Dinophysideae were represented also by colourless holozoic forms which produced still smaller populations, presumably resulting from light and temperature slowing down their metabolic processes.

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A Preliminary Study of the Energy Budget of Lake Ontario¹

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ABSTRACT

Recent bathythermographic surveys carried out on the research vessel *Porte Dauphine* have provided estimates of heat content for Lake Ontario and permitted a preliminary study of its energy budget. The imbalance between the absorbed short wavelength sun and sky radiation, and the losses due to evaporation, sensible heat conduction and net long wavelength back radiation, result in heating of lake water from March to August and cooling from September or October to February. The peak heat content lags the peak surface temperature by about one month. The amount of energy advected into the lake is relatively small compared with other terms in the energy budget. Thus, energy budget calculations do not depend upon the accuracy with which the water budget is known. The principal difficulty in applying present techniques for determination of an energy budget is lack of meteorological data over the lake surface.

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INTRODUCTION

THE DETERMINATION of the energy exchange between bodies of water and air constitutes one of the principal problems of oceanographic and limnological studies. Oceanographic studies of the energy budget are utilized for problems in seasonal temperature distribution, transport of energy by currents and the determination of water evaporation for quantitative calculations of elements in the hydrologic cycle (Sverdrup *et al.*, 1942). Limnological work has been undertaken principally for water loss investigations in reservoirs (see, for example, U.S. Geological Survey, 1954) and for predicting lake levels.

The present study was undertaken to determine the applicability of the energy budget method to the Great Lakes for the calculation of evaporation and the study of seasonal temperature changes.

In 1953 Blust, in an unpublished report of the United States Lake Survey, considered the various methods for determining evaporation, concluded that "... the heat budget method is superior for application to the Great Lakes ...", and made specific recommendations for carrying out initial studies. However, it has not been possible previously to make even a preliminary estimate of the energy (heat) budget for any of the lakes because of paucity of data and lack of continuity in observation. When, in 1958, R/V *Porte Dauphine* was made available on loan to the Ontario Department of Lands and Forests by the Royal Canadian Navy it became possible to start to supply the data and the continuity, to begin with, on Lake Ontario, for energy budget studies among other things. Presentation of some of the results was made by Bruce and Rodgers (MS, 1959).

The factors that must be considered in the energy budget are: short wavelength incident sun and sky radiation; reflected sun and sky radiation; long wavelength net back radiation; energy storage in the lake; energy contributions from inflow and outflow (including rain, rivers, snow and seepage); conduction of sensible heat and the energy used in evaporation. In this report all but the conduction and evaporation terms are evaluated individually with available data and by application of semi-empirical formulae presented in the literature. The sum of the conduction and evaporation terms is determined by balancing the energy budget (see equation 2) and dividing this sum between the conduction and evaporation processes in accordance with Bowen's ratio (Bowen, 1926; Sverdrup *et al.*, 1942).

Estimates of the average heat storage in the lake have been provided by bathythermographic surveys carried out on the *Porte Dauphine* during 1958 and 1959. These provide energy storage figures for late spring, summer and early fall periods in Lake Ontario. For winter months, the surface temperature data presented by Millar (1952) have been utilized, in conjunction with two assumptions concerning the vertical and horizontal temperature distribution within the lake, to provide energy storage figures.

Over-winter cruises were made for the first time in 1959-60, and heat content data from these have been included. As only one complete winter's data are available, and since that winter's air temperatures were somewhat milder than

normal, not as much weight was given these 1959-60 figures in comparison with the long-term meteorological averages and Millar's figures.

The energy budget calculations provide an estimate of the evaporation of water from the surface of the lake. The energy budget method is the third method to have been used to determine evaporation from Lake Ontario. The two methods used previously were the water budget and mass transfer methods (Hunt, 1959; Morton and Rosenberg, 1959; Kohler, 1959; Snyder, MS, 1960) and so the results from eight evaporation studies can be compared, providing a further check on energy budget results.

THE ENERGY BUDGET

GENERAL EQUATIONS

The energy budget for a specified time interval is expressed in the following equation:

$$Q_s - Q_r - Q_b - Q_h - Q_e + Q_v - Q_t = 0 \quad . . . (1)$$

Q_s is the amount of solar radiation incident to the water surface, Q_r the reflected solar radiation, Q_b the net back radiation, Q_h the conduction of sensible heat to the atmosphere, Q_e the energy in evaporation (or condensation), Q_v the net advected energy, and Q_t is the energy storage of the body of water considered. Energy abstracted and produced by chemical or biological activity, and heat exchange with bottom sediments are considered negligible.

In equation (1) values of Q_s , Q_r , Q_b , Q_v , Q_t can be obtained from meteorological and limnological measurements, so giving $(Q_h + Q_e)$. Similarly, from a relationship due to Bowen (1926), the ratio:

$$Q_h/Q_e = R \quad . . . (2)$$

can be determined independently, and then Q_h and Q_e each can be determined.

The accuracy of application of (2), in the present circumstances, is considerably less than the accuracy of the terms in (1) so that obtaining independent knowledge of either Q_e or Q_h would be a great advance.

Monthly means of daily values have been employed to give an average yearly cycle, and the terms in equation (1) were calculated in energy flux units of gram calories per square centimeter per day (g-cal/cm²/day).

The bathythermographic surveys were carried out in 1958, 1959 and 1960 whereas the surface temperature data given by Millar, and used here in the calculation of Q_t , Q_b and R , represent the period 1937-1946. Since these data do not necessarily represent similar periods, they have been uncritically coupled with long-term averages of meteorological elements at land stations around the lake. Meteorological data are required in the calculation of every term but Q_t .

The bathythermographic surveys covered all but the shallow outlet basin region in the east end of the lake (the region north of the Main Duck Islands), and so only the larger and deeper portion of the lake has been considered. The consequence of the outlet basin in the budget of the whole lake will await further study. Since shallow basins such as Saginaw Bay in Lake Huron and Green Bay in Lake Michigan, and the Lake Ontario outlet basin, may contribute heat

out of all proportion to their areas (and volumes), the neglect of the outlet basin in this case may be somewhat serious. A chart of the lake and the station pattern for 1959-60 surveys are shown in Fig. 1.

INCIDENT SOLAR RADIATION— Q_s

Monthly values of cloudless-day solar radiation and average daily incident solar radiation were obtained from charts prepared by Mateer (1955 a, b). A comparison of the two values for each month shows the effect of cloud cover on the incident solar radiation (see Fig. 2).

Some indication of the variation in incident radiation, from year to year, is shown in the figure by standard deviations derived from 20 years of radiation data (1938-1957) at Toronto, Ontario. The variation from year to year is caused principally by differences in cloud cover.

REFLECTED SOLAR RADIATION— Q_r

The reflectivity or albedo of a water surface under various sun altitudes, cloud heights and cloud amounts has been determined by Anderson (1954) in the Lake Hefner study. The average altitude of the sun for each month has been obtained by interpolation from tables in the Climatological Atlas of Canada (Thomas, 1953). Reflectivity was obtained from Anderson's graph for broken cloud conditions. Since Lake Ontario develops little ice cover, the amount of reflected radiation is a small portion of the energy budget.

NET BACK RADIATION— Q_b

Net back radiation is the resultant longwave radiation exchange between the water and the atmosphere. It is dependent upon air and water temperatures, the water vapour content of the air, cloud heights and cloud cover. The Lake Hefner study (Anderson, 1954) resulted in a semi-empirical equation for atmospheric radiation which, when combined with the value for emissivity of water determined for that study (i.e., 0.970 ± 0.005) and corrected for reflected atmospheric radiation, may be summarized into the form (Tabata, 1958):

$$Q_b = 1.141 [T_w^4 - T_2^4(a + be_2)] \times 10^{-7} \text{ g-cal/cm}^2/\text{day} \quad \dots (3)$$

where T_w and T_2 are the absolute temperatures of the lake surface and air, respectively, at 2 metres' height, and e_2 is the vapour pressure of the air in millibars at 2.0 m. The parameters a and b take on values dependent upon cloud cover and cloud height found from empirical expressions given by Anderson (1954),

$$a = 0.740 + 0.025 \text{ } C e^{-0.584h} \quad \dots (4a)$$

$$b = 0.00490 - 0.00054 \text{ } C e^{-0.060h} \quad \dots (4b)$$

where C is the cloud amount in tenths, and h the cloud height in thousands of feet.

Ten years of cloud height data (1949-58 inclusive) for Malton airport, which is 12 miles northwest of Toronto and 8 miles inland, were analyzed by the Data Processing Section of the Canadian Meteorological Branch for 0, 1 to 5, 6 to 9

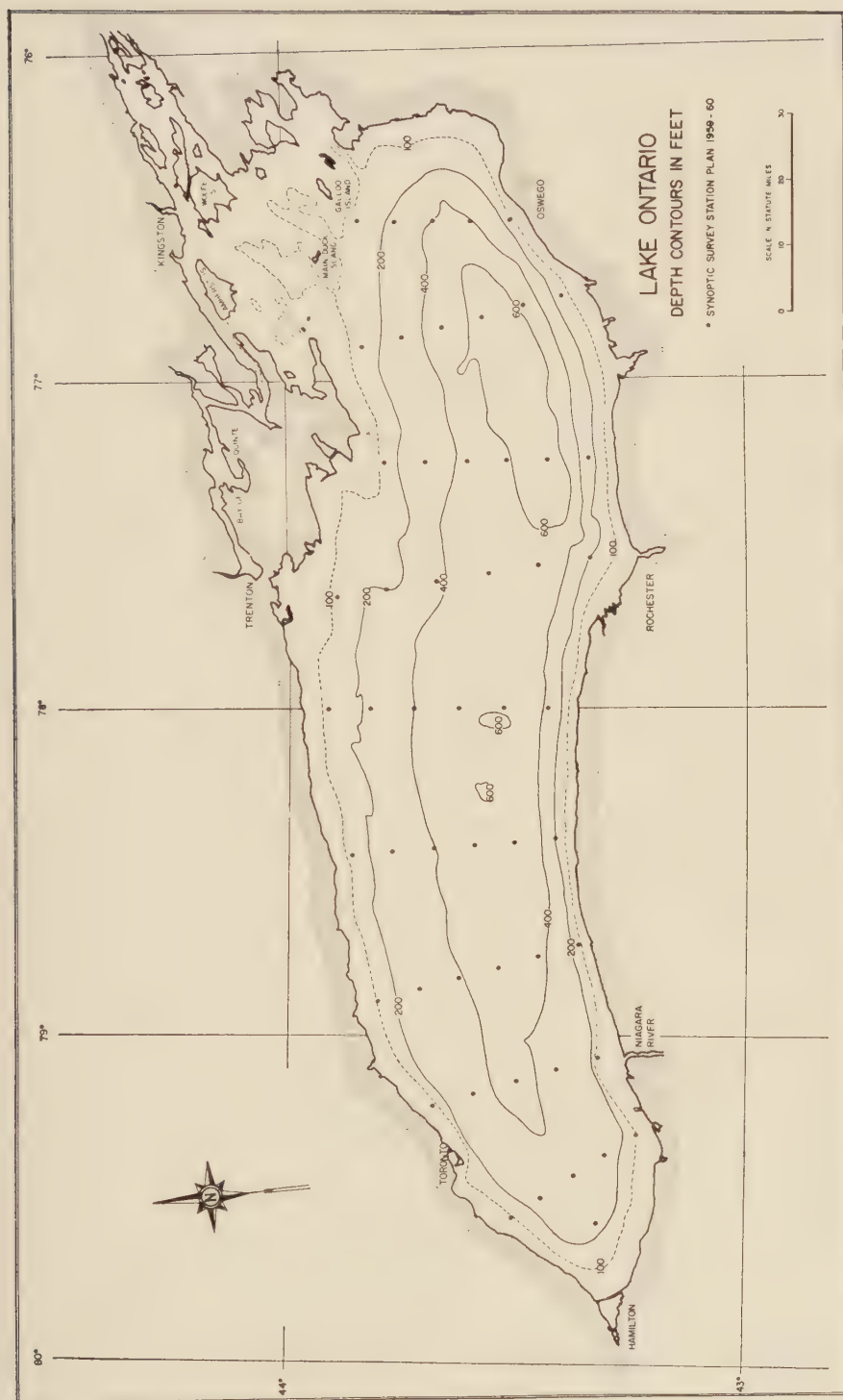


FIG. 1. Depth contours and station locations.

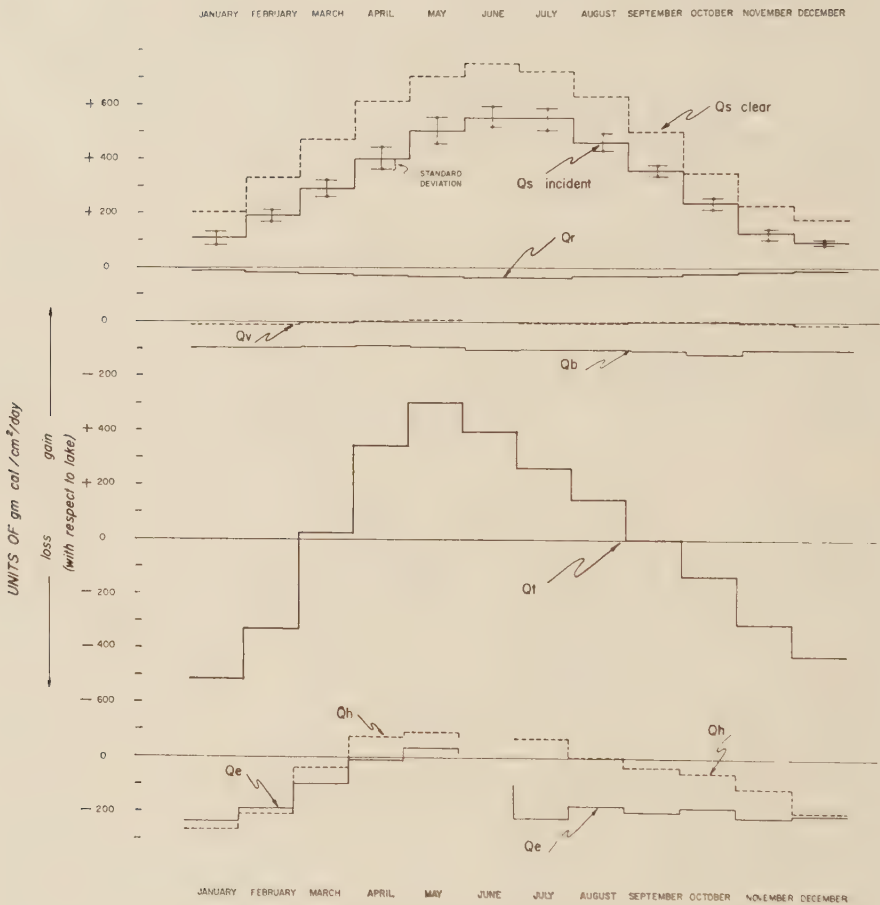


FIG. 2. Terms in the energy budget.

and 10 tenths cloud cover. The value for $(a + be_2)$ was calculated for each of these four cases and a weighted mean used for the calculation of representative values of Q_b for each month.

Air temperatures measured at the 2.5-metre level aboard the *Porte Dauphine* indicate that the 2-metre air temperatures must be much closer to surface water temperatures than to air temperatures measured at land stations. A particular example of this is shown in Fig. 3. There are insufficient data to provide a reliable conversion of land station temperatures to the air temperatures over the water. For this reason, T_2 has been quite arbitrarily taken as:

$$T_2 = T_w - (T_w - T_a)/4 \quad \dots (5)$$

This equation seems justified for summer conditions on the basis of the little data available, but does not necessarily hold well for winter conditions.

T_w was taken from Millar's data (Millar, 1952) and T_a (land station data) from the average between Toronto City and Rochester normal air temperatures (U.S. Dept. of Commerce, 1959). See Fig. 4 for T_w and T_a .

The vapour pressure also can be expected to be higher at 2 m over the water than at surrounding land stations. However, since its influence on the calculation of Q_b is probably less marked than that of temperature, no conversion has been attempted.

Months such as January, February, May and June in which $T_w - T_2$ is large have possible errors of ± 20 g-cal/cm²/day in this present study with less error during months when air and water temperatures are more nearly equal.

CONDUCTION OF SENSIBLE HEAT (Q_h) AND EVAPORATION (Q_e)

The transfer of heat may be treated similarly to the turbulent transfer of momentum and water vapour. But even if temperature profiles over the lake were known, there is still lack of understanding of details of the mechanism concerning the transfer. For this reason, Q_h is usually related to Q_e by the relationship (Bowen, 1926; Sverdrup *et al.*, 1942):

$$R = Q_h/Q_e = 6.1 \times 10^{-4} \left(\frac{p(T_w - T_a)}{e_w - e_a} \right) \quad \dots (6)$$

which is obtained by assuming that the transfer coefficients for heat and water vapour are the same. In equation (6), p is the atmospheric pressure in millibars, and e_w and e_a the corresponding vapour pressures in millibars. For lack of data over the water surface, land station data have been used for T_a and e_a . The monthly mean values of R listed in Table III appear to be large in comparison with those obtained in other studies of over-water conditions (Tabata, 1958; U.S. Geol. Survey, 1954; Sverdrup *et al.*, 1942). On the other hand data obtained at Lake Mead (U.S. Geol. Survey, 1958) suggest that it is immaterial where the air temperature and humidity are measured.

Another error may be due to the use of mean monthly data for computation of the Bowen ratio. A study in Australia (Webb, 1960) indicates the possibility of 5% error due to the fact that the vapour pressure-temperature relation is not linear.

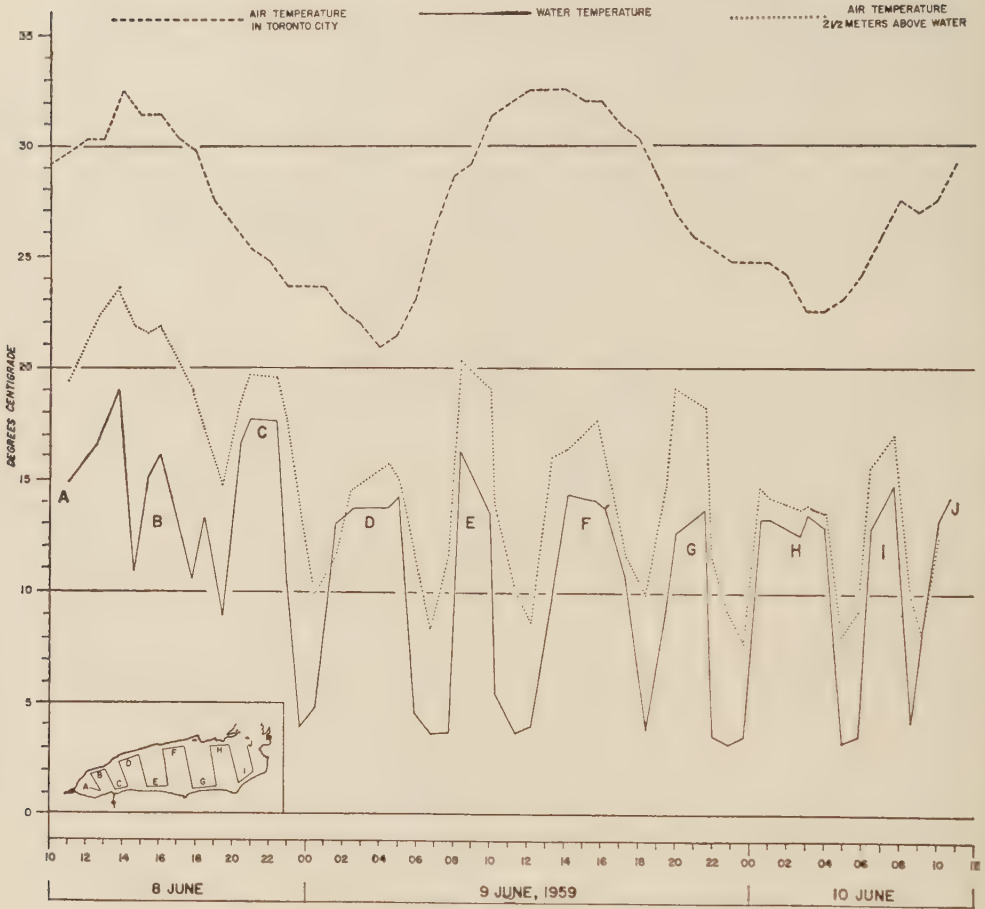


FIG. 3. Comparison of temperatures of air-over-land, air-over-water, and water.

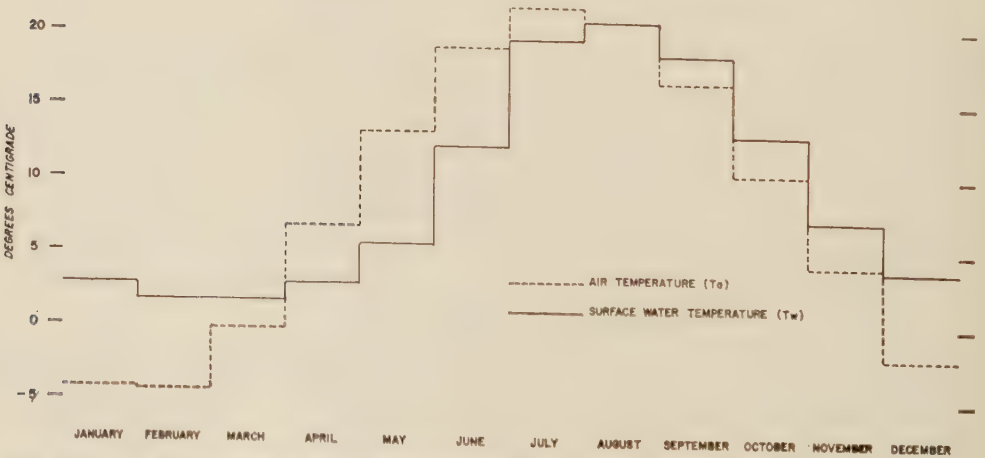


FIG. 4. Long term average monthly surface water temperature (T_w) and land air temperature (T_a). (T_w after Millar, 1952; T_a is the mean of values from Toronto and Rochester).

There appears to be net conduction of energy into the lake from April to July and out of the lake from September to May with maximum losses from the lake by this process in January and February.

ADVECTIVE TERM AND HEAT STORAGE— Q_v and Q_t

Q_v and Q_t cannot be treated independently since there must be continuity in masses of water entering, leaving, and stored in the lake. From the water balance alone heat is supplied to the lake (or abstracted) according to the following schedule:

Source or sink	Volume symbol	Temperature
Rainfall (total precipitation)	V_p	T_p , wet bulb temperature
Snow melt	V_s	Correction for latent heat of melting (heat loss = Q_m)
Niagara River	V_i	T_i
St. Lawrence River	V_o	At T_o (see Fig. 5)
Lake Ontario watershed	V_r	T_a (see Fig. 5) (in winter at 0°C)
Evaporation	V_e	At surface water temperature T_w

The average values of density d and specific heat c are, closely enough:

$d = 1.0$
 $c = 1 \text{ g-cal/cm}^2/\text{day}$

Thus we have:

$Q_v = (V_p T_p + V_i T_i + V_r T_r) - (V_e T_w + V_o T_o) - Q_m \dots (7a)$

or: $Q_v = Q_i - Q_o - Q_m \dots (7b)$

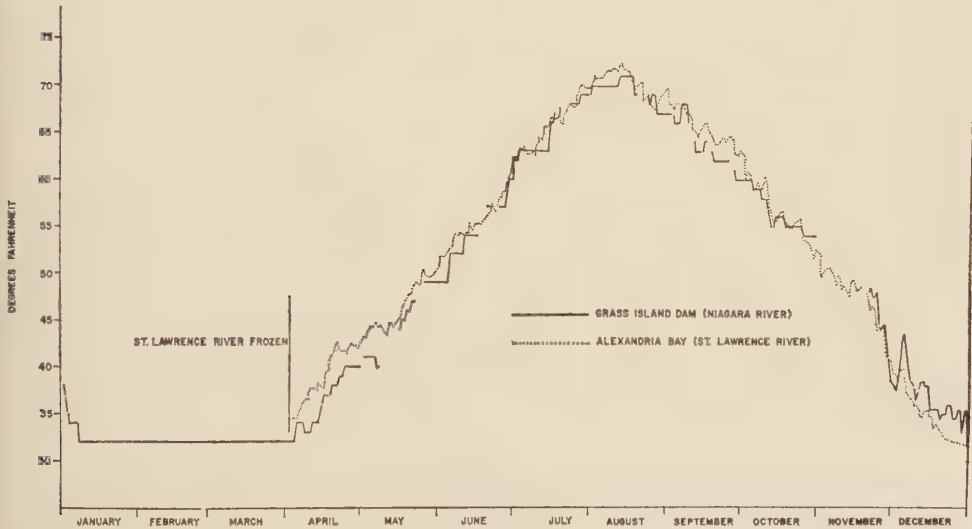


FIG. 5. Inflowing (Niagara River) and outflowing (St. Lawrence River) water temperatures.

If the volume of the lake at the beginning of the month is V_1 and its average temperature T_1 , and at the end of the month the values are V_2 and T_2

$$Q_t = (V_2T_2 - V_1T_1) \dots (8)$$

Since $(V_1 - V_2)/V_1$ is about 0.002 for the largest average monthly rise in lake level, very little error is made by using long-term average annual volumes for calculating T_1 and T_2 and thereby as well, Q_t . Monthly change in volume may be easily used, but the error introduced by ignoring it is negligible.

TABLE I. "Advective" terms in the energy budget, in g-cal/cm²/day.

Months	J	F	M	A	M	J	J	A	S	O	N	D
$Q_i - Q_o$	-1	-1	0	0	+1	+2	0	-3	-6	-2	-2	+1
Q_m	+11	+10	+6	+2	0	0	0	0	0	0	+4	+9
Q_v	-12	-12	-6	-2	1	2	0	-3	-6	-2	-6	-8

It is evident that the water budget terms do not have to be known with a great degree of accuracy for energy budget calculations in such a large lake (see Table I). The water balance of Morton and Rosenberg (1959) has been used in these calculations, including their estimate of V_e , since it is not critical in this calculation.

Q_t as defined in equation (8) has been drawn up from four sets of data, and is shown in Fig. 6. The four sets of data are:

- (1) Eight 1958 surveys of Lake Ontario (one survey of 10 stations and seven of about 30 stations);

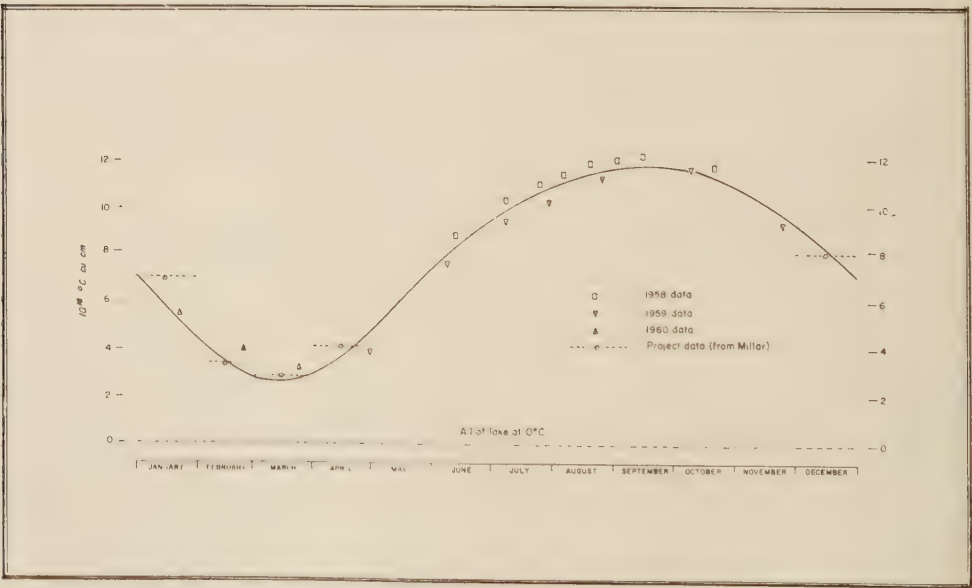


FIG. 6. Average monthly heat content.

(2) Nine 1959 surveys of the lake (one of 44 stations, one of 47 stations and seven of 52 stations);

(3) Average surface temperature transects of Lake Ontario for the months of December through April taken from Millar's (1952) work.

(4) Three winter surveys 1959–60.

In order to estimate winter energy content with the third set of data, two assumptions had to be made. It was assumed that the water had been vertically homogeneous in temperature and that this temperature was uniquely determined by the depth. Millar's temperature transects provide a temperature versus water-depth plot. The lake volume was then divided up into volumes corresponding to several depth intervals, and these volumes, at the temperature given by the temperature-depth graph, provide an estimate of heat content.

The assumption that the water is vertically homogeneous in temperature is supported by Church's work in Lake Michigan (Church, 1942), and by the Lake Ontario winter surveys of 1959–60. In the winter period water temperatures range from 0 to 8°C—a range in which the coefficient of thermal expansion is least for water. This means that the water is close to neutral stability and most easily mixed by winds.

Millar (1952) has noted the control of depth on surface temperature during months of near-neutral stability. This observation prompted the second assumption. If the advective term is small, if vertical mixing is efficient and horizontal mixing limited, and heating (or cooling) uniform over the lake, it is not unreasonable to expect depth control of temperatures in agreement with the observations of 1959–60.

In view of the above limitations, it is believed that the assumptions give reasonable estimates for February and March. The values for December, January and April were used only as guides in drawing the curve of heat content shown in Fig. 6.

The use of only two years' data for plotting the summer heat content and one year's data for the winter, in conjunction with long-term averages of meteorological elements and winter temperatures, should not be thought to imply that the heat content trend does not vary significantly from year to year. Much more work will be required to obtain a satisfactory complete seasonal cycle of heat content and its probable variations with which to correlate the prevailing meteorological conditions.

The time of maximum heat-content lags the time of maximum surface water temperature by about one month, during which time deeper penetration of heat is shown by the continuing rise of temperature at 50 feet (15 m), after surface temperatures have started to decline. Figure 7, showing the seasonal changes in temperature at several levels in the lake, illustrates this phenomenon.

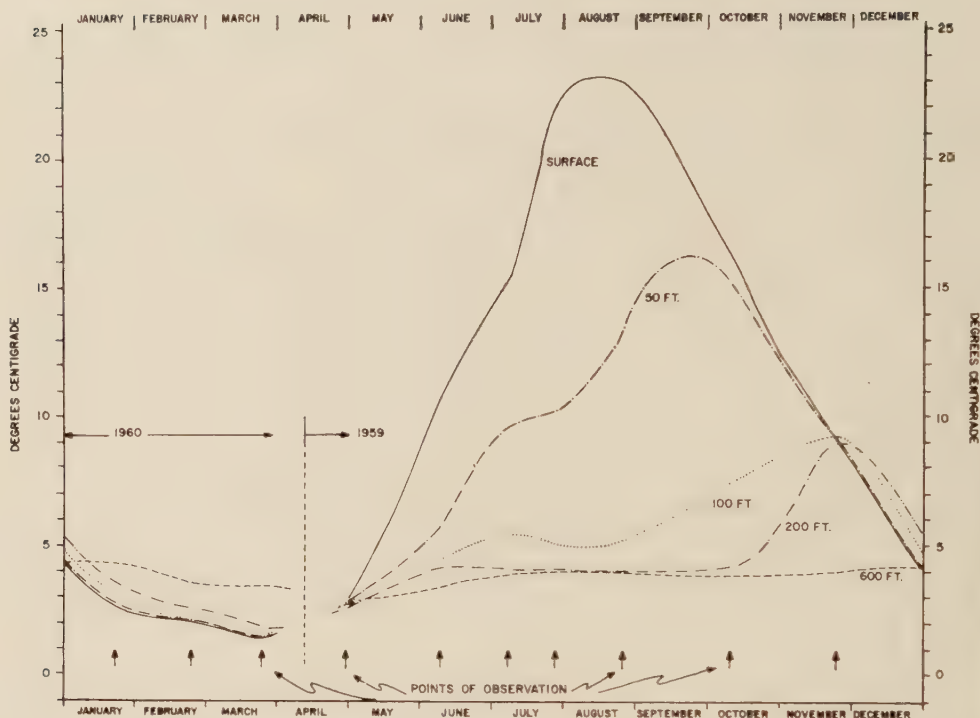


FIG. 7. Seasonal change in average temperature at several levels, 1959-1960.

EVAPORATION

The energy abstracted from the lake by evaporation also removes a certain amount of water from the system. This is given by

$$E = Q_e/dL \quad \dots (9)$$

where d is the density of the liquid and L the latent heat of evaporation. L for pure water is given by Sverdrup *et al.* (1942, p. 62):

$$L = 596 - 0.52T_w \text{ calories} \quad \dots (10)$$

where T_w is the temperature of the surface water in degrees Centigrade.

The evaporation E in terms of feet of lake level per month appears in Table V, with values from other studies for comparison. Q_e , as it appears in the energy budget, is given in Table II and Fig. 2. For the months of July to February, the evaporation varies little from 200 g-cal/cm²/day, or 0.33 feet per month. From the values of $(c_w - c_a)$ it appears that slight condensation may take place in May and June.

TABLE II. The energy budget of Lake Ontario, in g-cal/cm²/day. (See the appendix for explanation of symbols.)

$$Q_s - Q_r - Q_b - Q_e - Q_h + Q_v = Q_t$$

	J	F	M	A	M	J	J	A	S	O	N	D
Q_s	110	190	290	400	500	550	550	460	360	240	130	95
Q_r	13	18	24	28	33	35	36	31	28	22	14	12
Q_b	95	95	90	85	90	100	100	100	105	115	90	90
Q_t	-510	-330	25	345	505	400	265	150	0	-135	-305	-420
Q_v	-12	-11	-6	-2	1	2	0	-3	-6	-2	-6	-8
Q_h	260	210	40	-75	-95	?	-70	0	30	55	110	200
Q_e	240	185	105	15	-35	0?	220	175	190	180	215	205
$(Q_e + Q_h)$	500	395	145	-60	-130	15	150	175	220	235	325	405

TABLE III. Ancillary data. (See the Appendix for explanation of symbols).

	J	F	M	A	M	J	J	A	S	O	N	D
r	.115	.096	.081	.069	.066	.063	.065	.067	.077	.090	.108	.126
T_w °C	2.8	1.7	1.7	2.8	5.6	12.2	19.4	20.6	18.3	12.8	7.2	3.9
$T_w - T_a$ °C	6.9	6.1	1.4	-3.9	-7.6	-6.7	-2.2	0	1.8	2.5	3.0	5.9
RH %	82	80.5	76.5	72	71.5	71	71	72.5	76.5	78.5	80.5	81
$e_w - e_a$ mb	3.80	3.35	2.13	0.42	-1.76	-1.28	4.20	6.68	6.66	4.94	3.52	3.80
R	1.11	1.12	0.40	-5.71	2.65	3.21	-0.32	0	0.17	0.31	0.52	0.95

DISCUSSION

ENERGY BUDGET TERMS

Since the advective terms are small, the energy budget is almost independent of water budget determinations when monthly values are considered. The energy content change of the lake is determined therefore, by the imbalance of absorbed short wave-length sun plus sky radiation (i.e., $Q_s - Q_r$) and losses due to evaporation, conduction and net back radiation. The sum $(Q_e + Q_h + Q_b)$ indicates maximum losses in January when the absorbed radiation is close to the yearly minimum value of December (see Fig. 2). This same sum in May shows a slight gain in lake energy due to conduction or convection of energy *into* the lake and condensation of water vapour from the atmosphere—this at a time when the absorbed sun and sky radiation term is approaching the yearly maximum of June and July. The result is maximum heat loss in January, maximum gain in May and near-balanced energy exchange in the months of March and September.

ENERGY BUDGET CALCULATIONS

There are limitations to the accuracy of energy budget calculations as presented in this report. These are enumerated here, with suggestions for future improvement in more detailed applications of the technique. It should be emphasized again that these calculations represent an *average* energy budget. It is clear that substantial differences may occur from year to year in each term for any given month.

The limitation imposed by lack of data and empiricism of the formulae used is most evident in the results for the month of June. In this month the residual ($Q_e + Q_h$) is $+15$ g-cal/cm²/day, indicating that there is resultant energy loss from the lake. However, $(e_w - e_a)$ and $(T_w - T_a)$ indicate condensation, and conduction from air to water respectively, both giving energy *gain* for the lake. Fifteen g-cal/cm²/day is well within the possible error of calculations, but the magnitudes of $(e_w - e_a)$ and $(T_w - T_a)$ are such that perhaps an even greater miscalculation might have taken place. The error may be as much as 30 g-cal/cm²/day. Stable conditions in the layer of air over the water make an estimate difficult. This problem cannot be resolved until sufficient meteorological data have been collected over the water surface.

Comparison of the July evaporation values presented in Table V indicates that the value of Q_e for July is high, possibly because of the near-critical value of R . For values of R approaching -1 , Q_e becomes large. Thus any small errors in $(T_w - T_a)$ or $(e_w - e_a)$ are magnified in the calculation of Q_e . This again casts doubt upon the advisability of using land station data.

Of the terms individually calculated for the energy budget, the value of Q_b is probably the least reliable. The major source of error arises from the need for air temperatures at the 2-metre level in the application of equation (3). Again the need for meteorological data over the lake surface is indicated.

A secondary source of error in the calculation of Q_b might arise from the use of land station cloud height and cloud cover data rather than lake observations in the calculation of $(a + be_2)$ in equation (3). The Malton data are shown in Table IV. For comparison, the average cloud amounts for Rochester airport are also tabulated. As even these two sets of land data differ significantly from

TABLE IV. Comparison of cloud cover at two stations close to Lake Ontario.

	J	F	M	A	M	J	J	A	S	O	N	D
Malton ^a	7.5	7.0	6.6	6.2	5.8	5.7	5.2	5.3	5.3	5.3	7.2	7.4
Rochester ^b	8.1	7.8	7.2	6.7	6.7	5.9	5.5	5.6	5.6	6.1	8.0	8.1

^aAverage for the period 1949 to 1958 inclusive (data supplied by the Meteorological Branch, Canada Department of Transport).

^b18-year average (U.S. Weather Bureau, Publication No. 35).

one another, it will be necessary as well to determine lake cloud cover directly, and so find how it is related to land cloud cover. The lake produces its own cloud regime, the likelihood being that it is cloudier over the lake than on surrounding land in winter and less cloudy in summer.

The question of cloud cover is even more important in the determination of the incident solar radiation. Cloud cover reduces the total possible radiation (with continuously clear skies) by 50% in winter and 20 to 30% in summer. A one-tenth difference in cloud cover for a given month will alter the flux of incident radiation in winter by 20 and in summer by 80 g-cal/cm²/day.

It will also be necessary to have direct incident radiation measurements on the lake for periods even as long as one month. The location of such instruments

must be carefully planned to allow for likely disparity of land and lake cloud cover.

Lake ice cover in winter has not been considered in the calculations of this report, since Lake Ontario has substantial ice cover only in the outlet basin, which has been excluded. It affects both Q_b and Q_r . Usually, since ice surface temperatures can become colder than water surface temperatures, the Q_b , as

TABLE V. Evaporation of Lake Ontario, in feet of lake level per month. (1 foot = 0.305 m).

Method	Water budget		Mass transfer					Energy budget
Reference	Hunt 1959	Morton & Rosenberg 1959	Freeman 1926	Hunt 1959	Kohler 1959	Snyder 1960	Bruce & Rodgers 1959	This study
Jan.	.20	.27	.22	.23	.26	.26	.33	.41
Feb.	.10	.19	.22	.18	.21	.23	.27	.29
Mar.	.06	.07	.13	.18	.18	.14	.19	.17
Apr.	.03	.07	.09	.07	.08	.05	.05	.02
May	.02	.04	.02	0	0	-.05	-.11	-.06
June	-.02	.02	.09	.01	.02	.01	-.05	0
July	.09	.15	.31	.16	.19	.19	.24	.38
Aug.	.26	.33	.43	.21	.23	.33	.41	.29
Sept.	.32	.35	.38	.32	.32	.35	.53	.33
Oct.	.37	.38	.36	.27	.27	.31	.43	.31
Nov.	.34	.37	.20	.23	.22	.22	.33	.36
Dec.	.32	.37	.20	.20	.24	.25	.14	.35
Totals	2.09 ^a	2.61	2.65	2.06	2.22 ^b	2.28	2.76	2.85

^aWith the precipitation ratio $P_w/P_l = 1$, the annual total is 2.71 feet.

^bPan evaporation average of 6 stations (Kohler, 1959) gives an annual total of 2.39 feet.

calculated for this report, would be larger than the true back radiation term if ice cover were extensive.

The albedo of ice and snow-covered ice is much greater than that of a water surface. In respect of Q_r , where:

$$Q_r = r Q_s \quad \dots (11)$$

(r being the albedo) a new snow surface can give rise to an r as high as 0.80.

The lowest average surface water temperatures are given for the months of February and March, and ice cover would affect Q_r for these months. The lowest monthly average surface temperatures are 35°F (1.7°C), with the highest temperatures in mid-Lake (Millar, 1952). Thus it appears that a great deal of ice cannot occur. It is likely to be restricted to shallow waters (shorelines and shallow basins) and the deep waters are probably always free of ice. It is estimated that 10% coverage at the shoreline would be a maximum in the most severe winter. This ice cover might have an albedo (r) of 0.50. Thus, the effective r for February for the whole lake (excluding the outlet basin) would be 0.14 rather than the 0.10 used. Q_r would then be 28 instead of 20 g-cal/cm²/day. This is considered an upper limit to the possible error in Q_r introduced by neglecting ice cover.

Aerial ice reconnaissance was started by the Meteorological Branch of the Canada Department of Transport in January, 1960 and this will provide data on all the lakes for such problems in future.

Since the energy storage term is a major term in the energy budget, attention must be paid to the quality of surveys designed to provide energy content data for detailed study of specific periods of time. For example, small changes in the calibration of the bathythermographs of the order of one tenth of a centigrade degree can change Q_t by 30 g-cal/cm²/day. Use of reversing thermometers to check bathythermograph readings is necessary in order to reduce this error. An alternative is to use a more sensitive recorder such as the TPR (Temperature Profile Recorder) instrument, described in the Lake Hefner study (Anderson, 1954).

Another possible error in Q_t may result from the fact that the surveys are quasisyntoptic. The 1959 surveys required about 40 hours to complete. The presence of an internal seiche may cause apparent heat content values to be too high or too low depending on the state of the seiche, the direction of the wind and the pattern of the stations chosen. An estimate can be made of the magnitude of the error incurred by neglecting internal seiches, the effect being greatest during the summer stratification. A uninodal seiche in a simplified two-layer system, with an epilimnion 50 feet (15 m) deep at 20°C and a hypolimnion at 4°C, has a period of about 12 days in Lake Ontario. If the internal seiche has a maximum full amplitude of 10 feet (3 m) at each end of the lake, if one of the surveys defining the heat content at the end of a one-month period takes 2 days (travelling from one end of the lake to the other), and if the time of this survey coincides with the time of maximum vertical movement of the temperature boundary, the apparent Q_t could differ from the true Q_t by 20 g-cal cm²/day for 2 surveys one month apart.

The evaporation determined from energy budget calculations follows the seasonal trend obtained by other methods (see Table I); that is, appreciable evaporation from July to February, less evaporation in March, and little evaporation or slight condensation in April, May and June but the annual total evaporation of 2.8(4) feet (0.87 m) is the highest of all the estimates.

This estimate might be expected to be high in view of the possible errors considered above. The evaporation for June was taken as zero when the sign of $(e_w - e_a)$ and the results of some of the other studies suggest that slight condensation takes place. This might account for an over-estimate of about 0.03 feet (0.01 m). The energy budget value for July, as remarked upon above, is higher than those for other studies and may be due to the sensitivity of equation (2) for the critical value of the Bowen ratio (R approaching -1). The values from other studies suggest that E for July by the energy budget technique may be 0.10 feet (0.03 m) too high. These two possible positive errors of 0.1 would bring the annual total down to 2.7 feet (0.82 m), in approximate agreement with the higher water-budget and mass-transfer estimates. It must be emphasized, however, that the probable error of this average heat budget, which is certainly

more than 10%, and the magnitude of likely yearly variations from it, cannot yet be stated with any statistical certainty.

The particularly low values include Hunt's (1959) water budget calculation, and Hunt's (1959) and Kohler's (1959) mass transfer calculations. If Hunt's water budget values are recalculated on the basis of a ratio of 1.00 for precipitation-over-water to precipitation-over-land, the total annual evaporation becomes 2.71 feet (0.83 m). Hunt employed ratios of 0.59 to 0.92 with an annual average ratio of 0.79. Present evidence from northern Lake Michigan (Blust and DeCooke, 1960) is that seasonal differences may be as high as 10%, but the annual totals are nearly the same ($\pm 2\%$). There is no guarantee that this applies to all regions of the Great Lakes, but it does suggest that a 20% difference in annual total precipitation is probably excessive.

Hunt's mass transfer calculation would be revised upward if two pieces of data which he used were reconsidered. There is a fairly large discrepancy between the monthly average surface temperatures recorded by Millar (1952) and those used by Hunt for the winter months. Four surveys carried out by the *Porte Dauphine* on the pattern shown in Fig. 1 gave the following mean surface temperatures and temperature ranges. The monthly average temperatures given by Hunt and Millar are shown for comparison. These temperatures confirm Millar's data.

Date	Mean surface Temperature	Temperature Range	Mean monthly temp.	
	°F	°F	Hunt °F	Millar °F
Dec. 16-21, 1959	40.1	43.9 to 35.6	34	39
Jan. 20-24, 1960	36.7	40.2 to 32.3	32	37
Feb. 22-25, 1960	35.6	38.5 to 32.2	32	35
Mar. 23-26, 1960	34.3	36.0 to 32.4	35	35

Hunt recognized the need to adjust winds measured over land for application over the water. He extrapolated from land station data using information obtained at Lake Okeechobee, Florida. This information led Hunt to increase land wind data 5 to 35% to give over-water winds. An analysis of ship records provided by Lanczi (see Bruce and Rodgers, 1959) suggests that this increase should be between 55 and 85%. A recalculation incorporating Millar's surface temperatures and the larger over-water winds was carried out (Bruce and Rodgers, 1959); this, shown in Table V, gives the greater annual total of 2.7(6) feet (0.84 m). This estimate still contains the uncertainty of the use of land station data for the vapour pressure of the air over the water.

Kohler's mass transfer calculations are based on land station data and a formula developed in the Lake Hefner study. Disparity in the sizes of Lakes Hefner and Ontario probably invalidates the formula used, since a large lake produces its own "climate". This also may be the reason for Snyder's (1960) low value. The lake affects the temperature and water vapour content of the air masses flowing over the lake. Wind profiles over the lake differ from those over land due to different stability conditions and different surface roughness

parameters. Cloud development over the lake is different from cloud development over land. Each of these meteorological elements must be determined in order rigorously to apply present techniques for evaluating the energy budget of lakes as large as any of the Great Lakes.

Land stations provided the climatological data for this report. There are few climatological data available yet from the Lakes and modification of the land station data used for this study was therefore rather arbitrary.

Meteorological stations placed on exposed points of land and on islands provide useful information. Data provided by recording or by telemetering weather buoys in open waters could provide systematic climatological data which would be more easily treated than the data presently being collected by moving ships.

Finally, it is hoped that further research into the physics of interaction of the atmosphere and lake surface will reduce the empiricism of energy exchange relationships and improve the accuracy of their assessment.

ACKNOWLEDGMENTS

The authors wish to express appreciation for the assistance rendered by the Climatology Division, Meteorological Branch, Canada Department of Transport, particularly in regard to analysis of the cloud height and cloud amount data for Malton airport. Supplementary water temperature data have also been supplied by the Ontario Hydro-electric Power Commission, the United States Geological Survey, and the Metropolitan Toronto Works Department. The work was done as part of a program of Great Lakes research which has been supported by collaboration and help from many agencies, notably the Royal Canadian Navy, the Ontario Hydro, the Meteorological Branch of the Canada Department of Transport, the Hydrographic Service of the Canada Department of Mines and Technical Surveys, the University of Toronto, and various Canadian oil companies. Without their aid R/V *Porte Dauphine* would not have been obtained and this study would not have been possible.

The manuscript was read by the staffs of the Pacific Oceanographic Group of the Fisheries Research Board of Canada, the Institute of Oceanography at the University of British Columbia, the Meteorological Branch of the Department of Transport, and the Lake Survey of the United States Army Corps of Engineers, and their criticisms are gratefully acknowledged.

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APPENDIX: List of symbols

Symbol	Description
a	parameter defined by equation 4a.
b	parameter defined by equation 4b.
C	cloud cover.
d	density.
e_2	vapour pressure of water in the air at 2.0 m above the water surface.
e_w	vapour pressure of saturated air at the temperature, T_w .
E	mass of water evaporated.
h	cloud height.
L	latent heat of vaporization of water.
P_w	precipitation over water.
P_l	precipitation over land.
Q_b	net back radiation.
Q_e	energy involved in evaporation.
Q_h	conduction of sensible heat to the atmosphere.
Q_i	energy flow of water masses entering the lake.
Q_m	heat loss involved in converting snow at 0°C. to water at 0°C.
Q_o	energy flow of water masses leaving the lake.
Q_r	reflected solar radiation.
Q_s	solar radiation incident to water surface.
Q_t	energy storage of the body of water.
Q_v	net advected energy.
r	albedo of the water surface.
R	Bowen ratio defined in equation (2).
T_a	air temperature measured at a land station.
T_w	surface water temperature.
T_2	air temperature at 2.0 m above the water surface.
T_p, T_o, T_1 and $T_2, V_e, V_i, V_o, V_p, V_r, V_s, V_1$, and V_2 are all defined in the text, page 625.	

NOTES

Muscle Proteins of Pacific Salmon (*Oncorhynchus*) **I. A Note on the Separation of Muscle Proteins Soluble** **in Low Ionic Strength Salt Solutions**

Whole extracts of fish muscle proteins soluble in salt solutions of low ionic strength have been studied by several groups of investigators. Connell (1953) and Nikkilä and Linko (1955) have between them carried out a general survey of the electrophoretic properties of muscle proteins of fishes of various biological types, representing a total of about 25 species. Hamoir (1951, 1954, 1955a, b) and Henrotte (1952, 1954, 1955) have studied the carp muscle proteins extensively, and Dingle and associates (1955) the Atlantic cod (*Gadus callarias* L.) by electrophoretic methods.

The Pacific salmon (genus *Oncorhynchus*), however, have not been studied in this respect. The present communication describes the separation of muscle proteins of Pacific coast spring salmon (*O. tshawytscha*) by the use of diethyl-aminoethyl (DEAE) cellulose columns and also some electrophoretic studies of the proteins.

The protein extract was prepared by chopping the muscle tissue into small pieces and homogenizing in a Waring Blendor with 10 volumes of a 0.05 ionic strength phosphate buffer of pH 7.5, similar to that used by Connell (1953). All operations were carried out at 0°C and all glassware was pre-chilled. The blendor jar was loosely fitted with a plexiglass baffle plate extending just below the surface of the liquid to eliminate the vortex (Dyer *et al.*, 1950). Homogenization was carried out for ten 10-second intervals spaced sufficiently apart to allow the larger particles to settle towards the blades of the blendor. The blendor was operated at its high-speed position with a variac setting of 50 volts. The homogenate was centrifuged at 3000 g for 30 minutes in a Servall Type RC-2 automatic refrigerated centrifuge and the supernatant stored at 0°C. This protein solution was dialyzed exhaustively against the appropriate buffer at 0°C and centrifuged at 10,000 g for column chromatography and at 144,000 g for electrophoresis.

DEAE cellulose column methods have been used for the purification from lingcod (*Ophiodon elongatus*) muscle of a variety of enzymes (Tomlinson, 1959; Tarr, 1959; Martin and Tarr, 1961). In all these instances a convex type of gradient elution was used. In view of the success achieved in these experiments, whole extracts of salmon muscle proteins were separated by means of DEAE cellulose columns (Fig. 1). In this case, however, a concave upward type of

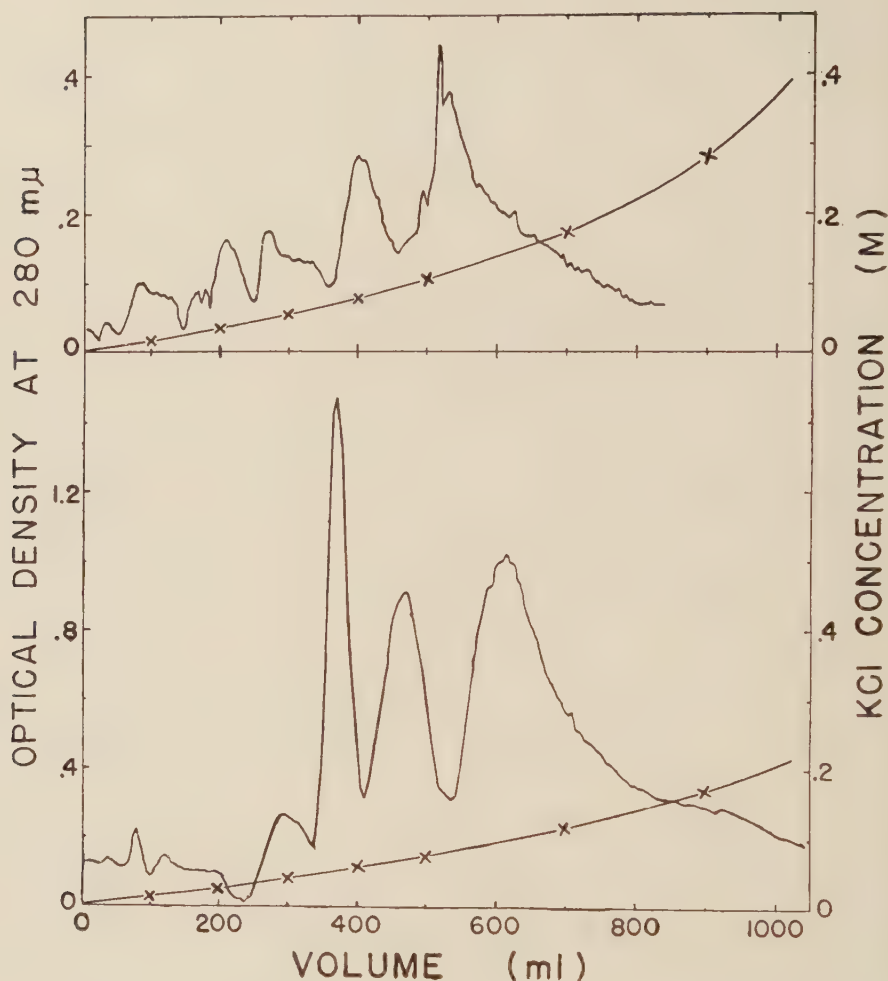


FIG. 1. DEAE column separation of salmon muscle proteins soluble in low ionic strength salt solutions. The spring salmon weighing approximately 5 lb each were caught by troll at sea and held for 8 hr in a tank under anaesthesia (tricaine methanesulphonate). The fish were then killed and filleted immediately. A portion of the fillets was extracted immediately and the remainder were sealed in polyethylene bags and stored at -35°C .

Upper. 9.0 g of DEAE Type 20, capacity 0.85 meq/g (Carl Schleicher and Schuell Co. Keene, New Hampshire) was packed in a 1.4-cm diameter column to a height of 45 cm in 0.001M Tris-HCl pH 8.5, and washed with several bed volumes of this solution. The protein extract (258.8 mg protein) was applied to the column and eluted by concave upward type of gradient with increasing concentrations of Tris pH 8.5 and KCl at a temperature of 0°C . The crosses represent the potassium chloride concentration gradient. Five-ml fractions were collected by a G.M.E. Model 10 Fraction Collector.

Lower. 13.0 g of DEAE packed to a height of 65 cm in a column of the same diameter as above and in a similar manner. Protein extract (573 mg protein) was applied and eluted as before.

gradient elution was used in order to obtain a more gradual increase in the salt concentration during the beginning of the elution. Sudden increases in concentration as would be expected by stepwise elution were avoided since such techniques may lead to artifactual peaks (Sober and Peterson, 1958). Preliminary experiments indicated that at pH's below 5.0 there was considerable precipitation of the protein extract, while at 7.5 the protein was not retained on the column. In contrast, the water-soluble lingcod muscle proteins purified initially by ammonium sulphate precipitation were retained at pH 7.0 (Tomlinson, 1959; Tarr, 1959; Martin and Tarr, 1961). At pH 8.5, however, the salmon proteins remained soluble and were retained on the DEAE column. Elution with increasing concentrations of potassium chloride and Tris-HCl (tris(hydroxymethyl)aminomethane) resolved the proteins into at least ten components (Fig. 1, upper). Storage of the protein extract at -35°C caused some precipitation of the small components eluting earlier when compared with the larger components coming off the column later (Fig. 1, lower). The use of a longer column (Fig. 1, lower) increased the resolution somewhat. Column chromatography, therefore, provides a simple technique of high resolution for the separation of fish muscle proteins soluble in low ionic strength salt solutions.

Electrophoresis of salmon muscle proteins using a Spinco Model H Electrophoresis Diffusion apparatus at pH 6.5, ionic strength 0.15 (0.1M with respect to sodium chloride) phosphate buffer showed little tendency for the proteins to migrate. Under similar conditions, the seven identifiable protein components from post-rigor cod muscle extractable with low ionic strength salt solutions show a range of values from 8.4×10^{-5} to $0.82 \times 10^{-5} \text{ cm}^2 \text{ volt}^{-1} \text{ sec}^{-1}$ (Dingle *et al.*, 1955). This indicates considerable differences in the properties of the proteins between the salmon and the cod. At pH 8.0 phosphate buffer of ionic strength 0.05 the salmon proteins showed the presence of seven components after a 6-hr run. The mobility values were found to fall within the limits of -0.95×10^{-5} to $-2.85 \times 10^{-5} \text{ cm}^2 \text{ volt}^{-1} \text{ sec}^{-1}$. Runs were not made at pH's lower than 6.0 since considerable precipitation was obtained.

These studies are being continued and further details of these experiments will be reported at a later date.

ACKNOWLEDGMENT

The authors extend their appreciation to Dr M. E. Reichmann of the Canada Agriculture Research Station at Vancouver for the electrophoretic analyses.

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Received for publication March 24, 1961.

Temperature and the Biochemical Processes Occurring During Rigor Mortis in Cod Muscle¹

The rapid biochemical changes which take place in muscle immediately post-mortem, especially the processes which occur during the onset and resolution of rigor mortis, have been widely studied in mammalian muscle. This work has been extensively reviewed by Bate-Smith (1948) and Whitaker (1959). Commercial fish species, however, have received little attention. Some early investigations were carried out on glycogen and lactic acid relations in trawled and hand-lined haddock, hake, cod and sculpin (Ritchie, 1926; MacLeod and Simpson, 1927; Leim, *et al.*, 1927; Macpherson, 1932; and Sharp, 1934). These workers showed that struggling reduced the muscle glycogen with accumulation of lactic acid, and concluded that the time of onset, the degree and duration of rigor mortis were dependent upon a number of factors, the most important being the method of catching. Later work has shown that an enzymic breakdown of adenosine triphosphate (ATP) by actomyosin ATPase or apyrase occurs in fish muscle (Partmann, 1954; Golovkin and Pershina, 1957), but apart from a few observations on frigate mackerel by Amano *et al.* (1953), no published data appear to exist on the deamination of adenosine nucleotides with the liberation of ammonia.

The interrelation of these biochemical processes associated with rigor mortis in fish muscle has not been established as yet. To elucidate these relations, the rate and extent of the breakdown of glycogen to lactic acid, the dephosphorylation of ATP, the deamination of adenosine nucleotides to inosine nucleotides with the liberation of ammonia, and the time to onset of rigor have been studied in Atlantic cod (*Gadus morhua*) muscle at various temperatures.

Rested cod held in a large aquarium at the laboratory were used. Struggling normally associated with death was reduced to a minimum by anaesthetizing the fish in a 0.1% solution of MS222 (Tricaine methanesulphonate; Sandoz Pharmaceuticals) prior to filleting. The metabolites were extracted immediately by homogenizing the muscle with six volumes of ice-cold 3% perchloric acid, followed by filtration and washing of the residue with additional 3% perchloric acid.

The changes in ATP (7-minute acid-labile phosphorus (LePage, 1949)) and in ammonia content of rested cod muscle held at temperatures of 0, 9, and 25°C after death are shown in Fig. 1. The onset of rigor occurred much earlier at the higher temperatures; post-mortem times at 0, 9, and 25°C were 12, 6, and $\frac{1}{2}$ hours respectively. Similar times to onset of rigor were found in a more extensive investigation of the effect of temperature and other factors influencing rigor in cod fillets (Dyer and Fraser, 1961). In eight samples of aquarium-held cod, the initial ATP content ranged from 27 to 40 mg P per 100 g muscle. This corresponded to an average of 5.2 micromoles ATP per g, which compared favourably with the value of 5.34 reported by Jones and Murray (1960) in rested cod muscle.

¹This work was presented in part at the Annual Conference of the Maritime Section of the Chemical Institute of Canada, Wolfville, N.S., September 9, 1960.

During the pre-rigor period the ATP disappeared rapidly, the process occurring more quickly at the higher temperatures. A similar temperature effect was observed by Saito and Arai (1957) who reported a more rapid dephosphorylation in carp muscle held at 16°C than at 0°C. Deamination of the adenosine nucleotides to inosine nucleotides with the liberation of ammonia accompanied the dephosphorylation. This process also occurred very much faster at the higher temperatures. Initial ammonia content ranged from 2.7 to 4.5 mg N per 100 g muscle, and increased to 10 to 11 mg N per 100 g during the resolution of rigor. The dephosphorylation and deamination occurred simultaneously, as has been reported for rabbit muscle by Bendall and Davy (1957). Deamination was substantiated by a change in the ultraviolet absorption maximum of the extract from 258 to 248 m μ , characteristic of adenosine and inosine nucleotides respectively. The rates of dephosphorylation and of deamination at 0°C observed in cod muscle are considerably slower than those found in trout muscle by Saito *et al.* (1959). This may indicate that the enzyme activity is less in the more sluggish cod.

The effect of temperature on the rate of glycogen depletion and of lactic acid formation is shown in Fig. 2. Initial glycogen values for rested cod from the aquarium were usually less than 0.1%, and the amount of lactic acid formed rarely exceeded 0.2%. In contrast, Sharp (1934) found initial glycogen contents of 0.6 to 0.85% in resting haddock; no reliable figures are available for cod muscle. The low glycogen values are probably due to the starved or semi-starved condition of the fish, since they were held at a water temperature near 0°C where feeding does not occur (MacKenzie, 1938). Thus, little muscle glycogen is available for degradation to lactic acid, and consequently the ultimate pH values during rigor remain near 7 (the so-called "alkaline" rigor). In the majority of these cod, the pH was initially 7.2 to 7.5, and it did not fall below an ultimate value of 6.9 as rigor was resolved. Similar high ultimate pH values were reported by Love (1958) with cod starved for long periods. However, Black *et al.* (1960) did not find the expected lowered muscle glycogen after starvation of trout for 3 to 7 days.

In Fig. 2, the very marked effect of temperature on the rate of glycolysis is illustrated. Lactic acid formation continued actively beyond the point of onset of rigor at each of the three temperatures investigated, 0, 9 and 25°C. At 25°C lactic acid formation had not reached the maximum even at 4 hours, whereas full rigor had been established at between 40 minutes and 1 hour. These results do not support the conclusion of Tomlinson *et al.* (1961) that maximum formation of lactic acid has been completed by the time of full rigor at temperatures near 20°C in unexercised rainbow trout (*Salmo gairdneri*) and Pacific coast starry flounder (*Platichthys stellatus*).

During this work, a few samples of otter-trawled cod and haddock, quickly frozen in brine after catching, were found to contain almost no glycogen. It was also observed that very rapid glycolysis, accompanied by dephosphorylation and deamination, occurred during thawing of a sample of rested cod muscle frozen in the pre-rigor state.

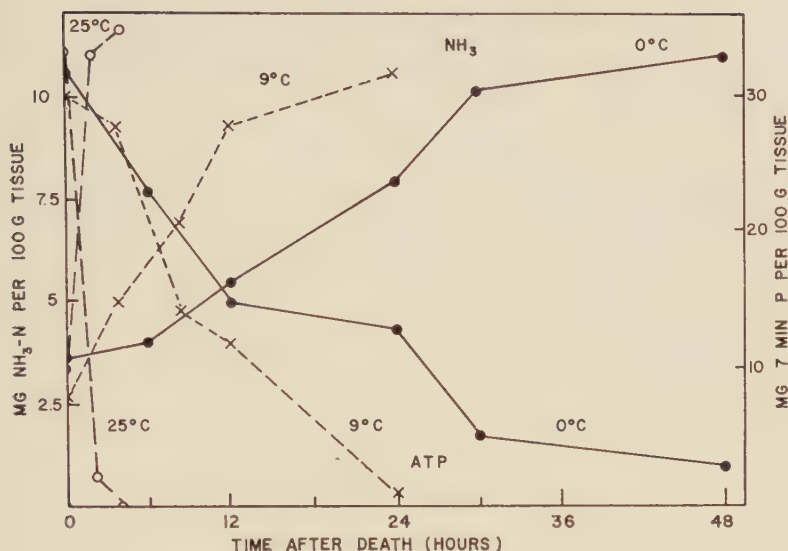


FIG. 1. ATP and ammonia changes in rested cod muscle at 0, 9, and 25°C.

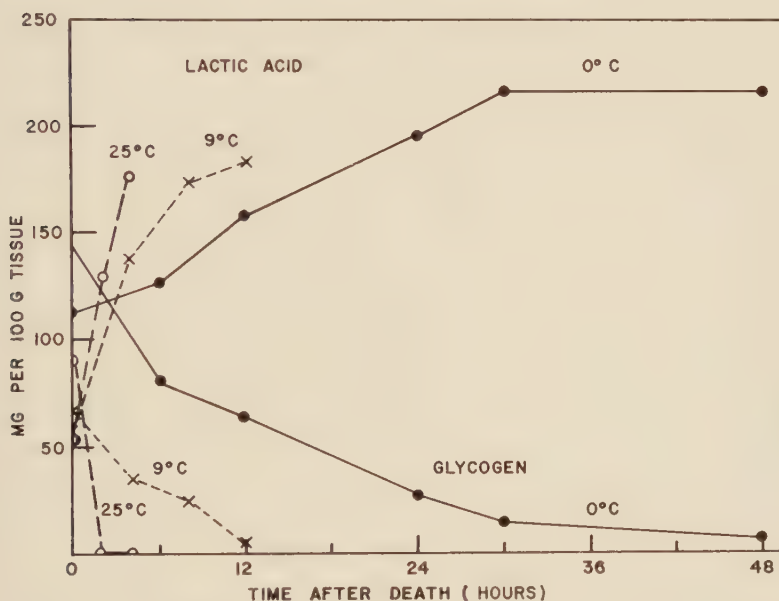


FIG. 2. Glycogen and lactic acid changes in rested cod muscle at 0, 9, and 25°C.

In conclusion, temperature markedly affected the rate of glycolysis in cod muscle; dephosphorylation and deamination of the adenine nucleotides occurred simultaneously with glycolysis. These processes were complete in about 30 hr at 0°C, 12 hr at 9°C, and in just over 2 hr at 25°C. In view of the increasing amounts of pre-rigor fish being processed industrially, the importance of these

changes associated with rigor mortis is becoming clearer. Our increasing knowledge should lead to the solution of some of the difficulties encountered in processing very fresh fish.

ACKNOWLEDGMENT

The authors wish to thank Dr J. E. Stewart for obtaining the samples of trawled cod and haddock during the March 1960 trip of this Board's research vessel *A. T. Cameron*.

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Received for publication April 24, 1961.

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Studies on Estimation of Mortalities

I. Comparison of a Method Described by Beverton and Holt and a New Linear Formula¹

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ABSTRACT

A method, described by Beverton (1954) and Beverton and Holt (1956 and 1957), giving estimates of the natural mortality rate, M , and the catchability coefficient, q , from catch at age and effort data, is examined. This method requires 4 to 5 iterations to arrive at the estimates. We have derived approximate solutions for q and M in a closed form. This makes the laborious iterations unnecessary, and gives virtually the same values as arrived at by iterations.

The effectiveness of the iterative Beverton and Holt method is evaluated by calculating q and M in 30 hypothetical examples. A new and simple (linear formula) method for estimating q and M is derived. Application of the new method to these 30 examples resulted in a 48% reduction in the standard deviation of q and a 45% reduction in that of M . The new method is in part the same as one suggested by Gulland, Beverton, and Holt (Beverton *et al.*, MS, 1958; Holt, MS, 1959) to arrive at initial values in their short-cut (iterative) method of estimating the mortality rates. Thus we show that these initial values are actually better estimates than the final values arrived at by the iteration.

Neither the Beverton and Holt method nor the linear formula give necessarily unbiased estimates; the bias depends on the types of variability in the data.

To arrive at non-biased, least squares estimates would require ancillary information not usually available on the distributions of the three variates: catch at age, effort, and catchability coefficient.

INTRODUCTION

CATCH OF FISH at age depends on the abundance of fish at that age and on effort expended for fishing operations. Other factors influencing the catch include the behaviour of fish, their distribution, and particular techniques or strategies used by the fishing vessels. In estimating mortality rates, these latter factors are not generally assumed to affect the average relationship between the abundance of stock, the effort expended, and the resultant catch. There are exceptions. Thus Holt (MS, 1957) has considered the effect of co-operation among the fishing vessels on their fishing efficiency but in general such studies have not been carried far enough to assess their practical importance. To arrive at the well known average relationship, termed here the "catch equation" (cf. equation (4)), it has been stated that the fish or the fishing operations should be randomly distributed; moreover, their distributions should be independent (cf. Ricker, 1940, 1944; Beverton and Holt, 1956). Additional, while perhaps not so critical, assumptions are that fishing and natural mortality are spread evenly in time. The catch

¹Received for publication August 16, 1960.

equation, based on the above assumptions, contains three unknown parameters: population size, what is called catchability coefficient, and instantaneous natural mortality rate; and two observed or directly estimated statistics: catch and effort.

The catch equation is basic to many estimation procedures in fisheries. DeLury (1947) used it to estimate the population size and the catchability coefficient. Silliman (1943) employed it to arrive at values of natural mortality rate. Silliman's method requires that the fishery be observed at two definitely different levels of fishing, each of at least two years' duration. More general methods for estimating the natural and fishing mortalities have been given by Widrig (1954), Beverton and Holt (1954, 1956), Fry (1949; MS, 1957), and Paloheimo (1958). The method employed by Widrig is similar to that by Beverton and Holt excepting that he does not carry the iterations beyond the first step. This iterative method is here referred to as the Beverton and Holt method, as they were first to describe it fully. The second method is referred to as the virtual population method, the name given to it by Dr Fry. Bishop (1959) has published a critique of the virtual population method. Her criticisms, however, were taken care of by the modification in the method by Paloheimo (1958).

The Beverton and Holt, and virtual population methods have been applied to few fisheries. The author is aware of only three fish stocks where the mortality rates have been so calculated. These are the Opeongo lake trout fishery (Beverton, 1954; Paloheimo, 1958), the Georges Bank haddock fishery (Taylor, 1958), and the South Bay bass fishery (Watt, 1959; this paper applies the earlier version of the virtual population method). Rounsefell's salmon data (Rounsefell and Kelez, 1938; Rounsefell, 1949) give rise to some difficulties, even if the Beverton and Holt method has been applied to it, due to the fact that Rounsefell's figures on escapement do not take account of the natural mortality rate.²

While applications of these general methods have not been very numerous, nevertheless, catch-per-effort data are widely collected, and apparently we may expect many more attempts to apply them.

Fisheries data are often subject to considerable sampling error and to deviations from the basic assumptions of the model. It is not always realized that before a method for estimating, say mortality rates, is developed, we must know the type of error inherent in the observation data. A method, which does not take account of such variability in data, may lead to biased estimates. Examination of the Beverton and Holt and virtual population methods shows that both are rather sensitive to the types of errors met in catch and effort data, and hence, may fail to give good estimates of the catchability coefficient and natural mortality rate; the bias is dependent on the type and magnitude of errors.

In the literature we find only descriptive accounts of the errors to which catch at age and effort data and the catchability coefficient are subject, and

²Beverton (personal communication) has pointed out that several other important applications of the Beverton and Holt method have actually been made. These include applications to East Anglian herring fishery (Cushing, 1959), and the Arctic cod and haddock fishery (Beverton *et al.*, MS 1959).

indeed, the estimation of error variances from field data does not seem feasible. Hence, any statistical method for estimating mortality rates may lead to somewhat biased estimates. The best method is the one which is least sensitive to types of variations met in fisheries data.

In this paper, we have concentrated on the study of the Beverton and Holt method. Its effectiveness has been calculated by estimating the catchability coefficient and natural mortality rate in 30 examples where random errors were introduced in the hypothetical data. In the examples considered, the method resulted in rather poor estimates of the natural mortality rate and of the catchability coefficient. The errors were large enough to warrant further examination. Since it was difficult to evaluate the effect of random errors in data on the estimates arrived at in successive iterations, we have derived approximate solutions of the natural mortality rate and catchability coefficient in a closed form. These solutions give approximately the same results as the iterative Beverton and Holt method, and they may be used to calculate the bias and standard deviations of the mortality estimates.

The method used to arrive at the approximate formulae may also be employed to derive an improved method for estimating the mortality rates. In the absence of a better name, the new method is termed here as the linear formula method. It is simple, requires no iterative procedure, and, in the examples calculated, resulted in a 48% reduction of the standard deviation of the catchability coefficient and a 45% reduction of the standard deviation of the natural mortality rate on the average.

The linear formula method has been suggested previously by Gulland, Beverton and Holt in some unpublished reports³ (cf., Beverton *et al.*, MS, 1958; Holt, MS, 1959) as a means for arriving at initial values of the natural mortality rate and the catchability coefficients thereby reducing the number of iterations required. Thus our results show that these initial values are really better estimates than the iterative Beverton and Holt estimates.

BASIC CONCEPTS

The following concepts and notations will be used⁴:

- j subscript, refers to the j^{th} age group. We will simply take $j = 1$ or 2 as an index of relative age.
- n number of years.
- i subscript, refers to year i , $i = 1, \dots, n$.
- $N_{j,i}$ numbers of the j -year-old fish at the start of the year i .
- $C_{j,i}$ numbers of j -year-old fish caught during the year i .
- f_i total effective effort during the year i .
- q catchability coefficient defined as the fraction of the population caught by one unit of effort; also the probability of capturing a fish.
 Subscript i or j will also be used for q to express its dependence on the year or the age.

³The author is obliged to both Holt and Beverton, who drew his attention to these reports when a draft of this current paper was submitted to them for comments.

⁴We are using the international notation (cf. Holt *et al.*, 1959).

- M instantaneous natural mortality rate.
 F_i instantaneous fishing mortality rate during the year i .
 Z_i instantaneous total mortality rate during the year i .
 t continuous time parameter, used primarily as a subscript.
 N_t total remaining population size at time t , the original population being N_0 .
 f_t total effort from time $t = 0$ to time t .
 C_t, Z_t, F_t are defined similarly.
 $\hat{q}, \hat{M}$ estimates of q, M .

The above concepts warrant some comments. To define the effective fishing effort, we consider two different types of fisheries separately. First, those in which only one method of fishing and one type of boat is employed; fisheries of this kind will be referred to as simple fisheries. Second, those in which more than one method of fishing or more than one kind of boat is employed; these fisheries will be referred to as complex fisheries.

In the case of simple fisheries fishing a uniformly distributed fish stock, the effective effort is the actual effort measured in terms of hours fished, hauls made or lines fished. If the stock is not uniformly distributed, but, if the area may be divided into subareas where this is the case, the effective effort is the weighted average of the efforts expended in the subareas; the weighing factors are taken as proportional to the catches per unit of effort in the respective subareas. In complex fisheries, two or more different kinds of effort units are employed. Methods of calculating the effective effort, in such a case, have been studied by Gulland (1955), and Beverton and Holt (1957). We will not go into details here.

While the stock density may vary from subarea to subarea, we assume that the catchability coefficient is the same for all areas, subject perhaps only to random fluctuations.

The basic concepts introduced above are interrelated. The following formulae go back to Baranov (1918) and Ricker (1940, 1944):

- | | |
|-----|--------------------------------------|
| (1) | $N_t = N_0 e^{-Z_t}$ |
| (2) | $F_t = qf_t$ |
| (3) | $Z_t = qf_t + M$ |
| (4) | $C_t = F_t N_0 (1 - e^{-Z_t}) / Z_t$ |

One of the basic assumptions implicit in the above equations is that fishing takes place independently of local concentrations of fish; i.e., that operators of the fishing vessels are not able to sense the presence of fish. In most commercial fisheries this is not the case. Thus, fish are detected by fish finders (loops), echo sounders, etc., and the prospects for a catch may be determined without actually making the haul. To what an extent this affects the basic equation is not known.

VARIATIONS IN THE BASIC PARAMETERS

To obtain unbiased estimates of parameters in a given (mathematical) relationship, a knowledge of the variability and observation errors inherent in the data is essential. In estimating mortality rates, our basic data are pairs of values C_{ji}, f_i . These data must be available at least for two age groups and for several years; the number of years required for a proper estimation depends on the accuracy of data. The parameters to be estimated are q and M . The relationship between these and the observational data (C_{ji}, f_i) from which q and M are estimated depends on the method. Thus the Beverton and Holt method uses different equations than the virtual population method.

The statistics C_{ji} and f_i are both subject to sampling error. Errors in C_{ji} may be due to errors in the total estimated weight of catch, in the estimated average weights, and in the estimated frequency of the j -year-olds. The total effort figure, f_i , is also subject to sampling error. In simple fisheries, it is a weighted average of efforts by subareas. The weighting factors should be proportional to the density of fish in each subarea; in practice, the catch per unit effort figures in each subarea are used. Hence, the total effort is only an estimate of what it is supposed to represent. In complex fisheries, the effort is a weighted total of efforts expressed in different units, the weighting factors being the sample estimates of the relative efficiencies of different units of effort.

Fluctuations in the catchability coefficient may be divided into systematic, long-term, short-term, and random variations. Systematic variations in q may result from a different behaviour pattern associated with the age or size of fish (Ricker, 1940; Gulland, 1955). Under long-term or short-term variations, we include the changes in q due to changes in weather, hydrographic conditions, etc. Properly random variations from the average value of q arise primarily from the random or contagious distribution of fish.

It is obvious that q is not constant but a variable. In estimating q we may only estimate its average value.

DESCRIPTION OF AND COMMENTS ON THE BEVERTON AND HOLT METHOD

Beverton and Holt derive from catch equation (4) their basic equations:

$$(5) \quad qf_i + M = \log_e \left(\frac{C_{1i}/f_i}{C_{2i+1}/f_{i+1}} \right) + \log_e \left(\frac{Z_i (1 - e^{-Z_{i+1}})}{Z_{i+1} (1 - e^{-Z_i})} \right)$$

If the catchability coefficient q is different at ages 1 and 2, then the above equation should read⁵:

$$(6) \quad q_1 f_i + M = \log_e \left(\frac{C_{1i}/q_1 f_i}{C_{2i+1}/q_2 f_{i+1}} \right) + \log_e \left(\frac{(q_1 f_i + M) (1 - e^{-q_2 f_{i+1} - M})}{(q_2 f_{i+1} + M) (1 - e^{-q_1 f_i - M})} \right)$$

Equation (5) contains the term $qf_i + M$ on the left side; the right side is an estimate of Z_i ; it depends on $C_{1i}, C_{2i+1}, f_i, f_{i+1}$ as well as on q and M . We will denote this function by $Z'_i(C_{1i}, C_{2i+1}, f_i, f_{i+1}, q, M)$ or simply by Z'_i .

⁵The term $\log_e (q_2/q_1)$ was accidentally omitted in Paloheimo, 1958, page 752.

Rewriting (5) in the abbreviated notation, we get:

$$(5') \quad qf_i + M = Z'_i(C_{1i}, C_{2i+1}, f_i, f_{i+1}, q, M)$$

To estimate the values of q and M in equation (5') from the statistics on catch and effort, an iterative procedure is used. Initial values of q and M are first guessed at, or estimated, from the regression of $\log_e(C_{1i}/f_i)/(C_{2i+1}/f_{i+1})$ on f_i (cf. (5)) as the slope of the line (q) and the intercept (M) at zero effort. The initial values of q and M are then used to calculate new values of Z'_i and a new regression line of Z'_i on f_i is obtained. The slope of the line and the intercept at $f = 0$ are the new estimates of q and M respectively. Substituting the new values of q and M in the expressions for Z'_i gives improved estimates for Z'_i which may be used in turn to arrive at a new regression line and improved estimates of q and M . The iteration is continued until the resulting q and M converge to fixed values which are then the final estimates of q and M .

BIAS IN THE MORTALITY ESTIMATES. Successive estimates of q and M , at each iteration, are given by the slope and the intercept, at $f = 0$, of the regression line of Z'_i on f_i . Substituting f_i and Z'_i in the familiar regression formula, we get:

$$(7) \quad \hat{q} = \frac{(n-1)(\sum f_i Z'_i) - (\sum f_i)(\sum Z'_i)}{(n-1)(\sum f_i^2) - (\sum f_i)^2} \quad \hat{M} = \frac{(\sum f_i^2)(\sum Z'_i) - (\sum f_i)(\sum Z'_i f_i)}{(n-1)(\sum f_i^2) - (\sum f_i)^2}$$

where summations are from $i = 1$ to $i = n-1$.

It is well known that the use of regression techniques in fitting the straight line $Z'_i = qf_i + M$ assumes that f is free of error and q is constant. Deviations from these assumptions will lead to bias in the estimate of the slope and intercept of the line. Further complications result because of the fact that Z'_i is dependent on f_i, f_{i+1}, q , and M .

For a discussion of different techniques of fitting a straight line, we refer to Kendall (1957), Williams (1959) and Madansky (1959). If both Z'_i and f_i are subject to error, $Z'_i = qf_i + M$ is not a regression model but a functional relationship and an entirely different technique should be used to arrive at the estimates of q and M . If nothing more about f_i and Z'_i is known than their observed or calculated values, the line cannot be properly fitted. Efficient techniques of fitting a straight line, when errors in Z'_i and in f_i are not independent but correlated, are not known.

Let Δf_i and Δq_i denote possible error in f_i or relative variation in q (i.e., $q_i = q(1 + \Delta q_i)$). Consider first, the case when f_i is subject to observational error. Then, in equation (7), the term $(n-1)\sum f_i^2$, originally assumed to be without error, has actually been inflated by $(n-1)\text{var}\Delta f$ and the term $(n-1)\sum f_i Z'_i$ by $(n-1)\text{cov}(Z, \Delta f)$. These correction terms should be subtracted from the corresponding terms $(n-1)\sum f_i^2$ and $(n-1)\sum f_i Z'_i$ to arrive at non-biased estimates of q and M for fixed values of Z'_i .

In the case where q is variable but f_i is free of error, considerations similar to those above apply. We may write $qf_i = q(1 + \Delta q_i)f_i$ and consider that the error actually occurs in f_i, f_i being the observed value and $(1 + \Delta q_i)f_i$ its true

value. Minor deviation results in the fact that the variance of f_i is now correlated with f_i . Hence, the term $(n-1)\Sigma f_i^2$ must be decreased by the factor $(1 + \text{var } \Delta q)$ and the term $(n-1)(\Sigma f_i Z'_i)$ by the additive constant $(n-1)\text{cov}(1 + \Delta q, Z')$ to arrive at non-biased estimates of (the average) q and M .

Formula (7) results in efficient and unbiased estimates of q and M for fixed Z'_i only when the regression model strictly applies. When it does not, additional components of error in q and M are introduced by having the values of q and M on the right side of (5) fixed (in Z'_i) while fitting the regression line of Z'_i on f_i and, also, by the fact that the errors in the right and left side of (5) are not independent. This may be seen from the approximate formulae we will derive for the Beverton and Holt iterative estimates.

APPROXIMATION FOR EQUATION (5). Equation (5), which Beverton and Holt solve by iterative methods, may be solved approximately in a closed form. We first write equation (5) in the form:

$$(8) \quad qf_i + M = I_i + K_i = Z'_i$$

where:

$$I_i = \log_e \left(\frac{C_{1i}/f_i}{C_{2i+1}/f_{i+1}} \right)$$

$$K_i = \log_e \left(\frac{Z_i(1-e^{-Z_i+1})}{Z_{i+1}(1-e^{-Z_i})} \right)$$

We may approximate K_i by a simple expression:

$$(9) \quad K_i \sim -\frac{Z_{i+1}}{2} + \frac{Z_i}{2}$$

where we have written:

$$(10) \quad -\log_e \frac{1-e^{-Z}}{Z} \sim \frac{Z}{2}$$

by expanding $\log_e(1-e^{-Z})/Z$ as an infinite series and retaining only the first term. In Table I we have tabulated the values of $-\log_e(1-e^{-Z})/Z$ and of $Z/2$ for $0.10 \leq Z \leq 1.00$. Between the values $0.2 \leq Z \leq 1.00$, which is the likely range

TABLE I. Values of $\log_e(1-e^{-Z})/Z$.

Z	$Z/2$	$-\log_e(1-e^{-Z})/Z$	Z	$Z/2$	$-\log_e(1-e^{-Z})/Z$
0.10	0.05	.0492	0.60	0.30	.2850
0.20	0.10	.0982	0.70	0.35	.3297
0.30	0.15	.1462	0.80	0.40	.3724
0.40	0.20	.1933	0.90	0.45	.4165
0.50	0.25	.2395	1.00	0.50	.4587

$Z = 1.00$

$\Sigma \log_e(1-e^{-Z})/Z$

Note: $Z = 0.20$

$0.20 + 0.30 + \dots + 0.90 + 1.00 \sim 0.47$

for most mortality estimates, the values of $Z/2$ are somewhat higher than those of $-\log_e(1-e^{-Z})/Z$. Thus if we write in general:

$$(10') \quad -\log_e \frac{1-e^{-Z}}{Z} \sim aZ$$

$$(9') \quad K_i \sim -aZ_{i+1} + aZ_i$$

the best value for "a" varies slightly depending on the range of the Z_i values. While for all practical purposes we could take $a = 0.5$ in applications, nevertheless, a somewhat smaller value of "a" gives a slightly better approximation. We have chosen $a = 0.47$, which is its average value between $0.2 \leq Z \leq 1.00$, obtained from Table I by calculating:

$$(11) \quad a = \frac{-\sum \log_e(1-e^{-Z_i})/Z_i}{\sum Z_i}$$

where the summation is over the values of $Z_i = 0.2, 0.3, \dots, 0.9, 1.0$.

Equations (8) and (9') allow us to approximate the basic Beverton and Holt equation in the form:

$$(12) \quad \begin{aligned} qf_i + M &= I_i + a(Z_i - Z_{i+1}) \\ &= I_i + qa(f_i - f_{i+1}) = Z'_i \end{aligned}$$

The iterative procedure to estimate q and M in (5) leads to estimates of q and M which, when substituted in (7), satisfy it. Hence, substituting approximations (12) in (7), the final value of q satisfies.

$$\hat{q} = \frac{(n-1)(\sum f_i I_i) - (\sum f_i)(\sum I_i) - \hat{q}a(\sum f_i)(f_1 - f_n) + \hat{q}(n-1)a[\sum f_i(f_i - f_{i+1})]}{(n-1)\sum f_i^2 - (\sum f_i)^2}$$

From this we may solve for $\hat{q}$:

$$(13) \quad \hat{q} = \frac{(n-1)(\sum f_i I_i) - (\sum f_i)(\sum I_i)}{(n-1)(\sum f_i^2) - (\sum f_i)^2 + a(\sum f_i)(f_1 - f_n) - (n-1)a[\sum f_i(f_i - f_{i+1})]}$$

Summations are from $i = 1$ to $i = n-1$

When the value of $\hat{q}$ obtained from (13) and approximation (12) for Z'_i are substituted in expression (7) for $\hat{M}$, we get:

$$(14) \quad \hat{M} = \frac{(\sum f_i^3)(\sum I_i) - (\sum f_i)(\sum f_i I_i) + qa(\sum f_i^2)(f_1 - f_n) - qa(\sum f_i)[\sum f_i(f_i - f_{i+1})]}{(n-1)(\sum f_i^2) - (\sum f_i)^2}$$

Equations (13) and (14) provide satisfactory approximations to the iterative solution of equation (5) by Beverton and Holt in all cases where the iteration converges. Since (13) and (14) give solutions for q and M in a closed form, calculating time is reduced appreciably.

EXAMPLE I.

In Table II we have calculated, using data from Tables IX and X, the Beverton and Holt iterative estimates and the approximate estimates (13) and

(14) with $a = 0.47$. The maximum difference between the iterative estimates and the approximate estimates for M is 0.023 and for q is 0.004.

TABLE II. Comparison of Beverton and Holt iterative solutions of q and M and the approximate solutions of q and M by formulae (13) and (14). Data are given in Tables IX and X.

Example No.	Beverton and Holt		Approximate	
	$\hat{q}$	$\hat{M}$	$\hat{q}$	$\hat{M}$
1	.073	.354	.075	.344
2	.071	.334	.073	.326
3	.119	.091	.122	.076
4	.210	-.389	.206	-.363
5	.008	.774	.008	.752
6	.091	.225	.094	.213
7	.122	.059	.125	.046
8	.127	.052	.129	.038
9	.054	.455	.055	.447
10	.155	-.094	.158	-.115

THE NEW LINEAR FORMULA

Equation (12) suggests a rather simple method for calculating $\hat{q}$ and M . By taking $a = \frac{1}{2}$ we may write the equation in the following form:

$$(15) \quad q \frac{1}{2}(f_i + f_{i+1}) + M = I_i$$

$$I_i = \log_e \frac{C_{1i}/f_i}{C_{2i+1}/f_{i+1}}$$

Regression estimates for q and M from (15) are now given by:

$$(16) \quad \hat{q} = \frac{(n-1)(\sum \bar{f}_i I_i) - (\sum \bar{f}_i)(\sum I_i)}{(n-1)(\sum \bar{f}_i^2) - (\sum \bar{f}_i)^2}$$

$$\hat{M} = \frac{(\sum \bar{f}_i^2)(\sum I_i) - (\sum \bar{f}_i)(\sum \bar{f}_i I_i)}{(n-1)(\sum \bar{f}_i^2) - (\sum \bar{f}_i)^2}$$

where $f_i = \frac{1}{2}(f_i + f_{i+1})$ and the summation is taken from $i = 1$ to $i = n-1$. If, in place of approximation (10) we use (10'), $\bar{f}_i = \frac{1}{2}(f_i + f_{i+1})$ should be replaced by $\bar{f}_i = (1-a)f_i + af_{i+1}$ where we could take $a = .47$. In practice, however, there seems to be so little difference between the results obtained by using the two alternatives for $\bar{f}_i$ that we have preferred the one which is algebraically simpler (i.e., $\bar{f}_i = \frac{1}{2}(f_i + f_{i+1})$).

COMPARISON OF THE BEVERTON AND HOLT METHOD AND THE NEW LINEAR FORMULA

Neither the Beverton and Holt (formulae (13) and (14)) or the linear formula method (16) give unbiased estimates of the mortality rates. Indeed, unbiased estimates cannot be obtained unless we know a good deal more of the under-

lying statistical nature of our data than is available from current fisheries data. In general, however, the estimates (16) are less biased and have a smaller variance than those obtained from (13) and (14).

The variance for $\hat{q}$ and $\hat{M}$ can be calculated from (13), (14) and (16). It should be noted that the often-used variance estimates (cf. Taylor, 1958; Beverton, 1954) obtained from the least squares fit of Z'_i on f_i are not valid estimates of the variance of $\hat{q}$ and $\hat{M}$.

To avoid cumbersome formulae we rewrite the approximate Beverton and Holt equations (13) and (14) as follows:

$$(17) \quad \hat{q} = \frac{D_1}{D_2}; \quad \hat{M} = \frac{E_1 + \hat{q}E_2}{E_3}$$

using substitutions D_1 , E_1 , E_2 , and E_3 for their obvious equivalents in the original formulae. For the linear formula estimates of q and M , written now as $\bar{q}$ and $\bar{M}$ to distinguish them from $\hat{q}$ and $\hat{M}$ in (17), we put similarly:

$$(18) \quad \bar{q} = \frac{\bar{D}_1}{\bar{D}_2}; \quad \bar{M} = \frac{\bar{E}_1}{\bar{E}_3}$$

Expansion for $\bar{D}_1$, $\bar{D}_2$, $\bar{E}_1$, and $\bar{E}_3$ can be obtained from (16).

The general order of magnitude of D_1 , D_2 , E_1 and E_3 is about the same as that of $\bar{D}_1$, $\bar{D}_2$, $\bar{E}_1$, and $\bar{E}_3$. A term equivalent to E_2 does not appear in the expression for $\bar{M}$; E_2 can be either positive or negative.

To compare the variance of $\hat{q}$ and $\hat{M}$ with those of $\bar{q}$ and $\bar{M}$, we distinguish four different possibilities, depending on whether (a) catches at age or (b) effort figures are subject to sampling error, or (c) the catchability coefficient is variable or finally (d) whether any combination of these three cases occurs.

If the catches at age data are the only observational data subject to sampling error and if the catchability is strictly constant, then formula (16) may not have any advantages over the Beverton and Holt method or formulae (13) and (14), because the variances of D_1 and E_1 are about the same as those of the corresponding expressions $\bar{D}_1$ and $\bar{E}_1$ and the covariance between $\hat{q}E_2$ and E_1 could possibly be negative and by absolute value as large as $\text{var}(\hat{q}E_2)$ (cf. (17)).

In all other cases, linear formula (16) has a definite advantage over the Beverton and Holt method or, what is the same thing, over formulae (13) and (14). This follows simply from the fact that we have replaced f_i in formulae (13) and (14) by:

$$\bar{f}_i = \frac{1}{2}(f_i + f_{i+1})$$

That is, if f_i 's are subject to sampling error while $C_{j,i}$'s are observed without error and q is constant then, since:

$$\text{var}\bar{f}_i = \frac{1}{4}(\text{var}f_i + \text{var}f_{i+1}) \sim \frac{1}{2}\text{var}f_i$$

the variances of $\bar{D}_1$ and $\bar{E}_1$ are reduced to about half of those of D_1 and $E_1(+qE_3)$. The variances of $\bar{D}_2$ and $\bar{E}_2$, compared with the variances of D_2 and E_2 , respectively, are reduced by more than half. This is because the $\bar{f}_i$'s and the

f_i 's appear as squares or cross products in $\bar{D}_2$, D_2 , $\bar{E}_2$ and E_2 . Thus the variances of $\hat{q}$ and $\hat{M}$ are, in turn, reduced by more than half from those of $\hat{q}$ and $\hat{M}$.

If q is subject to variation, the linear formula still has similar advantages because we may put $q_i = q(1 + \Delta q_i)$ but consider that, instead of error being in q , it is the f_i 's which are observed with error, the observed value being f_i and the true value $(1 + \Delta q_i)f_i$.

In the last case, when all three possible types of error are present, formula (16) has still advantage over (13) and (14) although the variances may not be reduced as much as before.

The improvement in the mortality estimates, which results from use of the linear formula (16), can be demonstrated by hypothetical examples.

EXAMPLE II. f_i 's SUBJECT TO ERROR

In this example, we have let $q = 0.10$ and $M = 0.10$, and calculated hypothetical catches for two years from 100,000 recruits each year, for a 10-year period. The values of f_i were allowed to vary between 4 and 8 units but were otherwise randomly picked from a table of random numbers. The values of f_i and the resulting catches are tabulated in Table III.

TABLE III. Hypothetical catches for 2 successive years from 100,000 recruits each year, over a 10-year period, with $q=0.10$ and $M=0.10$ and with expended efforts as shown.

Year	Effort	Catch	
		1st year	2nd year
1	4.00	31,476	
2	4.00	31,476	19,090
3	8.00	52,752	31,994
4	8.00	52,752	21,449
5	6.00	43,146	17,543
6	4.00	31,476	15,631
7	5.00	37,600	22,804
8	4.00	31,476	17,274
9	8.00	52,752	31,994
10	7.00	48,181	19,590

To introduce "observation error" in f_i 's in Table III, random normal deviates, read off from a table of random normal deviates (Deming, 1946) were added, properly scaled, to each f_i . The deviates, as read off from the table, were multiplied by $\frac{1}{2}$ to reduce the standard deviation of the error component to $\frac{1}{2}$ unit. Ten sets of (ten) f_i 's, $i = 1, \dots, 10$ were so picked, giving in conjunction with the C_{ji} 's 10 examples, each containing 10 years' hypothetical catch and effort data. The "estimated" efforts are tabulated in Table IV.

TABLE IV. Hypothetical fishing efforts. Figures obtained from the efforts in Table III by adding to each effort a random normal deviate with standard deviation 0.5.

Year	Example									
	1	2	3	4	5	6	7	8	9	10
1	4.09	5.14	3.65	3.33	3.89	4.22	3.30	4.14	5.11	4.01
2	3.89	3.47	3.72	3.27	3.43	4.64	3.49	3.48	3.89	3.82
3	7.94	7.66	7.82	8.04	8.36	8.28	7.36	7.65	7.44	7.47
4	7.95	7.23	9.08	7.93	8.09	8.37	7.41	7.63	8.38	8.10
5	6.22	5.81	7.06	6.70	5.18	6.19	6.05	6.62	6.00	5.21
6	4.20	3.08	4.42	4.46	3.31	4.44	4.09	3.57	4.30	4.48
7	4.52	4.91	3.56	5.04	4.81	5.63	5.33	4.85	5.05	5.23
8	3.44	3.41	3.79	4.61	3.86	4.23	3.52	3.07	4.31	3.85
9	8.01	7.88	7.60	9.04	8.55	7.78	8.29	8.14	7.87	8.44
10	7.39	6.59	7.02	6.58	6.73	6.01	7.37	6.71	6.76	8.04

The Beverton and Holt method and the linear formula (16) were applied to catches in Table III, and to the sets of efforts in Table IV, to arrive at the estimates of q and M . The correct values of q and M are $q = 0.10$ and $M = 0.10$. In applying the Beverton and Holt method⁶, the iterations were continued until the successive estimates of M changed less than .01 or of q less than .001. This usually required 4 or 5 iterations. The results are tabulated in Table V. It is to be noted that the linear formula (16) results in estimates of q and M , the variances of which, calculated from the known values of $q = 0.10$ and $M = 0.10$, are about 40% smaller for $\hat{q}$ and 38% smaller for $\hat{M}$ than the corresponding variances using the Beverton and Holt method.

TABLE V. Comparison of Beverton and Holt estimates and linear formulae estimates of q and M . Data are from Tables III and IV. The true values are $q=0.10$ and $M=0.10$.

Example	Beverton and Holt estimate		Linear formulae estimate	
	$\hat{q}$	$\hat{M}$	$\hat{q}$	$\hat{M}$
1	.100	.111	.123	-.026
2	.031	.475	.130	-.098
3	.078	.242	.103	.092
4	.051	.389	.074	.252
5	.028	.523	.072	.270
6	.107	.011	.096	.136
7	.073	.295	.111	.083
8	.050	.394	.143	-.131
9	.138	-.166	.147	-.220
10	.093	.156	.110	.052
Standard deviation of the estimates from the true value	.042	.251	.025	.155

⁶A LGP-30 computer was used.

EXAMPLE III. f_i 's SUBJECT TO ERROR

Data in Tables VI and VII are obtained the same way as the data tabulated in Tables III and IV respectively except that we have used $q = 0.10$ and $M = 0.20$ in arriving at the hypothetical catches at age.

TABLE VI. Hypothetical catches for 2 years from 100,000 recruits each year over a 10-year period, with $q=0.10$ and $M=0.20$, and with expended efforts as shown.

Year	Effort	Catch	
		1st year	2nd year
1	7.00	46,158	
2	6.00	41,298	16,792
3	5.00	35,955	15,155
4	4.00	30,080	14,938
5	5.00	35,955	19,732
6	4.00	30,080	14,938
7	6.00	41,298	22,664
8	5.00	35,955	16,155
9	7.00	46,158	22,922
10	8.00	50,568	20,561

TABLE VII. Hypothetical fishing efforts. Figures obtained from the efforts in Table VI by adding to each effort a random normal deviate with mean zero and standard deviation 0.5.

Year	Example No.									
	1	2	3	4	5	6	7	8	9	10
1	7.98	7.94	7.32	5.54	7.86	6.55	5.87	6.56	6.67	7.31
2	6.78	6.71	6.59	6.77	5.96	5.12	6.22	6.07	5.00	5.65
3	4.41	4.82	5.13	4.75	5.65	5.08	4.64	5.45	4.74	5.52
4	3.27	3.88	3.88	3.49	3.52	3.46	4.03	3.93	4.34	3.00
5	5.18	4.88	4.85	4.61	5.46	4.94	5.17	4.80	5.03	4.65
6	3.47	4.29	3.83	3.51	3.24	3.80	3.93	3.75	3.41	3.67
7	6.27	6.64	6.27	6.09	6.35	6.22	5.54	5.76	5.86	5.96
8	4.77	4.71	4.31	5.66	5.61	5.02	5.51	5.68	4.38	4.62
9	7.41	6.99	7.10	7.15	7.20	7.54	6.80	7.67	6.54	7.38
10	8.58	7.81	8.64	7.29	8.18	6.63	7.68	8.13	8.16	8.87

Application of the two methods considered here gives the values of $\hat{q}$ and $\hat{M}$ tabulated in Table VIII. The results confirm the conclusions from Example II, with 67% and 69% reductions in the standard deviations of $\hat{q}$ and $\hat{M}$, respectively, using the linear formula.

TABLE VIII. Comparison of Beverton and Holt estimates and linear formulae estimates of q and M . Data from Tables VI and VII. The true values are $q=0.10$ and $M=0.20$.

Example	Beverton and Holt estimates		Linear formulae estimates	
	$\hat{q}$	$\hat{M}$	$\hat{q}$	$\hat{M}$
1	-.007	.780	.069	.363
2	.029	.564	.067	.354
3	.046	.498	.108	.153
4	.021	.653	.079	.337
5	-.026	.886	.083	.269
6	-.024	.865	.038	.535
7	.110	.174	.105	.194
8	.084	.285	.081	.301
9	.035	.574	.119	.139
10	.007	.718	.089	.276
Standard deviation of the estimates from the true value	.084	.457	.028	.144

EXAMPLE IV. q SUBJECT TO VARIATION

In this set of examples, we have allowed q to vary from year to year in a random manner by adding random normal deviates of standard deviation 0.01 to the basic value $q = 0.10$. The resulting q 's are tabulated in Table IX. The hypothetical effort figures and the catches, corresponding to these efforts and catchability coefficients in Table IX, are tabulated in Table X.

TABLE IX. Hypothetical values of the catchability coefficient, q . Each figure is obtained by adding to $q = 0.10$ a random normal deviate with mean zero and standard deviation 0.01.

Year	Example No.									
	1	2	3	4	5	6	7	8	9	10
1	.0946	.0931	0.959	.1060	.0975	.0932	.1040	.0999	.0988	.1100
2	.1167	.0854	.1061	.1093	.1004	.0992	.0858	.1097	.1077	.0806
3	.0959	.1072	.0855	.0962	.1060	.0877	.1115	.1210	.1002	.1007
4	.1028	.1073	.1037	.0883	.1084	.1002	.0930	.0870	.1137	.0989
5	.1053	.1009	.0991	.0969	.0864	.0978	.0908	.0944	.0871	.1042
6	.1030	.0914	.0963	.0944	.1065	.1091	.1005	.0805	.0776	.1135
7	.1001	.1022	.1081	.1038	.0870	.1166	.1138	.1063	.0951	.1111
8	.1056	.0931	.1008	.0943	.0950	.0920	.0854	.0998	.1191	.1023
9	.1046	.0904	.0973	.1073	.0908	.0940	.0939	.0955	.0924	.1234
10	.1084	.0966	.0956	.0888	.1004	.1053	.1154	.1012	.0931	.0958

TABLE X. Hypothetical efforts and catches. Catch figures are calculated for 2 years from 100,000 recruits each year over a 10-year period, using effort figures and catchability coefficients varying randomly with each year and example. Catchability coefficients are given in Table IX, and $M = 0.20$. C_1 is catch at age 1; C_2 is catch at age 2.

Example No.: Effort	1		2		3		4		5	
	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2
7.00	44,366	...	43,887	...	44,789	...	48,065	...	45,366	...
6.00	46,153	19,490	36,623	15,620	43,151	18,063	44,081	17,183	41,404	17,121
5.00	34,828	14,161	37,935	18,615	31,779	18,760	34,885	14,819	37,615	16,867
4.00	30,747	15,576	31,857	15,253	30,986	16,537	27,116	13,723	32,139	15,488
5.00	37,441	20,327	36,231	19,318	35,739	19,328	35,118	20,200	32,017	18,985
4.00	30,806	14,895	27,954	13,815	29,155	14,534	28,716	14,473	31,657	16,829
6.00	41,349	22,428	41,952	23,816	43,733	24,359	42,459	23,815	37,168	19,877
5.00	37,496	16,832	34,019	15,091	36,175	15,479	34,367	15,091	34,544	16,785
7.00	47,611	22,996	42,957	22,071	45,265	22,393	48,464	24,751	43,105	21,945
8.00	53,303	20,991	49,423	21,484	49,071	20,335	46,618	18,009	50,693	21,970

Example No.: Effort	6		7		8		9		10	
	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2	C_1	C_2
7.00	43,887	...	47,429	...	46,115	...	45,786	...	49,288	...
6.00	41,059	17,512	36,792	14,548	44,173	17,974	43,593	17,865	35,061	11,586
5.00	32,434	14,641	39,119	19,137	41,545	17,615	36,013	15,453	36,175	18,250
4.00	30,138	15,910	28,336	13,278	26,792	11,981	33,385	16,562	29,846	14,765
5.00	35,351	19,383	33,328	18,807	34,367	19,868	32,254	16,753	37,120	20,446
4.00	32,254	16,188	30,197	15,699	25,087	12,812	24,283	12,858	33,328	16,207
6.00	46,153	24,438	45,366	24,851	43,198	25,629	39,807	23,904	44,559	23,166
5.00	33,670	13,690	31,722	13,177	35,915	15,537	41,106	19,012	36,623	15,440
7.00	44,173	22,833	44,127	23,573	44,697	22,210	43,640	19,682	53,179	26,095
8.00	54,479	23,099	55,446	23,531	50,990	21,385	48,192	20,660	76,600	26,435

The Beverton and Holt and linear formula estimates of q and M are tabulated in Table XI. The results show 37% and 27% reductions in the variances of $\hat{q}$ and $\hat{M}$, respectively, when the linear formula is applied.

TABLE XI. Comparison of Beverton and Holt estimates and linear formulae estimates of the mortality rates. Data from Tables IX and X. True value of $M = 0.20$, and q has the average value of $q = .10$.

Example	Beverton and Holt estimates		Linear formulae estimates	
	$\hat{q}$	$\hat{M}$	$\hat{q}$	$\hat{M}$
1	.073	.354	.083	.298
2	.071	.334	.057	.413
3	.119	.091	.110	.140
4	.199	-.327	.149	-.052
5	-.008	.774	.053	.438
6	.092	.225	.075	.315
7	.122	.059	.065	.375
8	.127	.052	.052	.465
9	.054	.454	.084	.287
10	.155	-.094	.121	.088
Standard deviation of the estimates from the true value	.054	.243	.034	.177

APPLICATIONS

The new linear formula (16) has been applied to Georges Bank haddock data (Taylor, 1958), and Fry's Opeongo lake trout data (Fry, 1949). Results are tabulated in Table XII. The standard deviations are the familiar regression estimates. While they are not strictly applicable here, more refined techniques (such as approximate least-squares estimates) have not been considered worth while due to the large error component. Indeed, the 95% confidence

TABLE XII. Linear formulae estimates of q and M of Georges Bank haddock fishery (data from Taylor, 1958), and Lake Opeongo trout fishery (data from Fry, 1949) and corresponding standard deviations. In brackets we have given Taylor's estimates for the Georges Bank fishery and, Paloheimo's (1958, using Beverton and Holt method) for the Opeongo trout fishery.

Age groups	$\hat{q}$	$\hat{M}$	Standard deviation	
			s_q	s_m
<i>Georges Bank haddock data</i>				
III and IV	.162 (.102)	-.574 (-.170)	.058	.414
IV and V	.051 (.085)	.242 (.012)	.040	.317
V and VI	.100 (.082)	-.082 (.004)	.061	.427
<i>Lake Opeongo trout fishery</i>				
IX and X	.050 (.047)	.339 (.374)	.030	.413

limits are so wide that it is questionable whether the estimates in Table XII have any practical value.

The Lake Opeongo trout fishery is a seasonal fishery, hence catch equation (4) or equations (5), (15) are not quite applicable since they have been developed by assuming a year-round fishery. To what extent the use of correct equations would change our results has not been studied. We also note that while the Georges Bank fishery is a year-round fishery, the catchability varies considerably from season to season. This variability may account for our poor estimates.

ACKNOWLEDGMENTS

I wish to thank Dr R. J. Banerji at the University of New Brunswick for the preparation of the program for the LGP-30 computer used in the iterative calculations. Mr Gordon S. Mann patiently carried out most of the other calculations required. Several colleagues, particularly Dr L. M. Dickie, have given valuable advice and criticism. Messrs Holt and Beverton kindly read the first draft and pointed out a few omissions on the part of the author.

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The Copepods *Calanus glacialis* Jaschnov and *Calanus finmarchicus* (Gunnerus) in Canadian Arctic-Subarctic Waters¹

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"CALANUS" SERIES, NO. 21

ABSTRACT

The literature on *Calanus finmarchicus* (Gunnerus) in arctic-subarctic Canada is reviewed, and the history of the 2-size-group phenomenon in the North Atlantic subarctic region is discussed. *Calanus glacialis* Jaschnov is briefly described, and compared with material from North America, the characters emphasized being size and the structure of the fifth legs. It is concluded that specimens from arctic and subarctic North America agree essentially with *C. glacialis*, those from the subarctic and north boreal regions with *C. finmarchicus*. Occurrence of the 2 species in northern North America is given, that of the large *glacialis* alone being shown to coincide closely with the known extent of unmixed polar water, of the 2 together to occupy the region of mixed polar and Atlantic water, and of the small *finmarchicus* alone to inhabit Atlantic water.

INTRODUCTION

THE COPEPOD *Calanus finmarchicus* has long been considered as one of the most abundant and most important planktonic species in all northern seas. Wilson (1932, p. 23) referred to the distribution of the species as: "Everywhere in all the oceans, including the Arctic and Antarctic. . . ." Ekman (1953) included it among the cold-water cosmopolites. Marshall and Orr (1955) listed many of the widely spread points of occurrence, and gave for it a temperature range of -2 to 22°C and a salinity range of 29 to 35‰. Northern waters however have provided the bulk of the material on the species, and a very large number of publications deal with *Calanus finmarchicus* of the North Atlantic and more northerly subarctic and polar waters. In 1955, Jaschnov described a new species, *Calanus glacialis*, from north Russian seas. Acceptance of this necessarily upsets the well established distributional picture of *C. finmarchicus* which *C. glacialis*, according to its author, replaces in arctic waters.

The considerable material on marine benthos brought to light by nineteenth-century explorers in the Canadian north did not extend to the smaller plankters, which were largely ignored until near the end of the century. One of the first references to *C. finmarchicus* is in Rodger's (1894) account of the marine fauna from off northeast Baffin Island. Although comparatively few references have followed, they have covered wide regions of both eastern and western waters of

¹Received for publication April 28, 1961.

northern Canada, and include Sars (1909), Willey (1920, 1923, 1931), Wilson (1936), Vibe (1950) and Johnson (1956). While these were concerned only with the occurrence of the species, 2 more recent works (Fontaine, 1955; Grainger, 1959) considered the biology of the species from Ungava Bay and Foxe Basin, respectively.

Early in the history of *C. finmarchicus* investigations the great length range of adults found in northern waters was noticed. Sars (1886) reported specimens from Jan Mayen of more than twice the size of the normal forms. In the Norwegian Sea, Gran (1902) noticed larger individuals in the north than in the south, and south of the Gulf of St. Lawrence, Willey (1919) reported a similar situation, the largest individuals being taken from the coldest waters. Currie (1918) found notably large specimens in the Bay of Fundy, and Willey (1920) only large individuals in and just east of the Beaufort Sea. Comments on the extreme size range from off West Greenland by With (1915) were followed by the recording by Størmer (1929) of 2 size groups of both adult females and stage V in the same area, the larger group described as occurring in northern cold, the smaller one in southern warm water. Jespersen (1934) expanded on the 2-group study, using females only, and showed the greatest proportion of large individuals in the north and west parts of Baffin Bay and along the coasts of Baffin Island and Labrador. He concluded that the large form was definitely associated with cold water. The demonstration of 2 size groups also was made from north of Spitzbergen by Farran (1936), and from East Greenland by Ussing (1938) and Jespersen (1939), the latter pointing out that large individuals were particularly numerous in deep (cold) water, smaller ones in surface (warmer) water. From north Foxe Basin, within the true arctic region of Canada, however, only large individuals, with no evidence of 2 size groups, were reported by Grainger (1959). It is perhaps significant that all the regions in which either great length variation or 2 length groups have been described fall either in or close to the subarctic marine area, as defined by Dunbar (1951), and that locations in which there is no evidence of either excessive length range or the 2-size-group phenomenon lie outside this area, both to the south and to the north.

Using material collected chiefly in the north Russian seas and data on length measurements from the literature, Jaschnov (1955) reviewed the *Calanus finmarchicus* problem and established as a result the new species named *C. glacialis* for members of the group previously recorded as "large" *finmarchicus*. Former "small" *finmarchicus* were retained as *C. finmarchicus* s.s. *C. glacialis* was designated the arctic form, and was listed as occurring in the Polar Sea, all Siberian seas, northern Barents Sea, cold waters of the Greenland Sea, White Sea and all the eastern Russian seas. *C. finmarchicus* s.s. was called a boreal species, occurring in the southern Barents Sea, off Norway, in the North Sea and over the North Atlantic.

Separation of the species was made on morphological grounds. Females of *C. glacialis* were given a total length range of 4.3 to 5.5 mm (cephalothoracic length therefore about 3.4 to 4.3 mm), and a ratio of body width to length of usually 1:2.7 to 1:3. The fifth legs were characterized by having along the inner

margin of their first segment a conspicuous concavity and large blunt teeth. The total length range of males was given as 4.7 to 5.2 mm (about 3.7 to 4.0 mm cephalothoracic length), and the fifth leg characterized by the relatively short endopodite not reaching farther than the middle of the second segment of the exopodite. In stage V, 3.2 to 4.7 mm total length (about 2.6 to 3.7 mm cephalothoracic length), the inner margins of the first segments of the fifth legs were described as showing clear concavities.

C. finmarchicus s.s. was described according to Sars (1901). Compared with *glacialis*, total length of females was given as 3.0 to 4.1 mm (cephalothoracic length therefore about 2.4 to 3.2 mm), and the ratio of body width to length as usually 1:3 to 1:3.5. The fifth legs were described as having the inner margin of their first segment either straight or very slightly concave, but not having the sharp inward curve of *glacialis*. The total length of males was given as 3.3 to 3.9 mm (cephalothoracic length about 2.6 to 3.0 mm), and the fifth legs characterized by the relatively long endopodite reaching as far as the distal third of the second segment of the exopodite. In stage V, 2.8 to 3.4 mm total length (cephalothoracic length about 2.2 to 2.8 mm), the inner margins of the first segments of the fifth legs were described as being straight or nearly straight.

In a later paper, Jaschnov (1957) discussed in greater detail than before other morphological characters, and analysed fifth leg tooth and bristle counts of several *Calanus* species. In particular, variations in the curve of the inner edge of segment one of the fifth legs of *C. finmarchicus* females were discussed, and it was pointed out again that while the typical form is either straight or perhaps slightly convex, a variation from this in which there is a slight inward curve exists. In another paper, Jaschnov (1958) discussed the origin of the "superspecies *C. finmarchicus* s.l.", proposing the development of *glacialis* during glacial times, and supposing its Pliocene ancestor also to have given rise to *finmarchicus* s.s. Brodsky (1959) has also recognized *glacialis* as a distinct species, and presents a map (his fig. 5) showing the distribution of *glacialis*, *finmarchicus* and other *Calanus* species.

It is perhaps remarkable that interpretation of the Russian workers should differ to such a degree from that of Jespersen (1934), who apart from Jaschnov had probably the most suitable collection for this study, and who stated (p. 31): "The two size groups of *Calanus finmarchicus* found in the West Greenland waters are undoubtedly to be regarded only as a larger and as a smaller form of the same species. For the most minute investigation of the different characters has failed to reveal differences beyond that of size and the relative dimensions incident to it." Jespersen reported average counts of 34.8 teeth for small individuals and 34.4 teeth for large individuals. No reference was made to any difference in shape or size of the teeth in the 2 groups.

MATERIAL EXAMINED

Specimens of *Calanus* from arctic and subarctic North America were obtained from several sources. The bulk of the material was from collections made from the M.V. *Calanus*, of the Fisheries Research Board of Canada, in the area between

Labrador, Hudson and James Bays, Foxe Basin and Cumberland Sound, Baffin Island. Many collections made from H.M.C.S. (later C.G.S.) *Labrador* among the islands of the Canadian archipelago and in Baffin Bay and Davis Strait were used as were collections made from the *Cancolim II* in the Beaufort Sea. Additional material was acquired from Ice Island T-3, north of the Canadian islands in the Arctic Ocean, from Pelly Bay, from the Labrador Sea, the Strait of Belle Isle and eastern Newfoundland, and from the Gulf of Maine. Several thousand specimens were included in the available material, measurements and morphological data being recorded for about 2000 individuals.

Length frequency histograms of a number of samples showed evidence of 2 size groups, of the majority of samples however of only a single group, either large or small. No single length was found to separate the large and small individuals over the whole area considered; instead there appeared to be a more or less consistent variation in the separating length related to geographical location.

In Fig. 1 are length frequency histograms of selected material measured, cephalothoracic length being given in micrometer units (0.126 mm). Collections from Ungava Bay show the most evident 2-group composition, the size groups being divided at 25 units (3.2 mm).

At the majority of locations only individuals of 25 units and greater length occurred, as shown on the left side and the upper right side of Fig. 1. In central Davis Strait, the Labrador Sea and the Strait of Belle Isle however there is shown a slightly greater mean length for the small group than was found in the other samples (lower right side of the figure). In a series of 5 collections extending from west Davis Strait (close to the Greenland coast) to near the northern tip of Labrador, there is a clear indication of increase in mean length of the small size group from the Greenland coast to central Davis Strait, and a nearly identical situation is shown in Jespersen's material taken along almost the same line, the largest of the small group occurring in central Davis Strait, the smallest near either coast. Jespersen's (1934) division between his 2 size groups was put at about 3.5 mm, apparently because only specimens from south Davis Strait were included in his fig. 5. Figure 2 here shows histograms from several of Jespersen's south central Davis Strait stations compared with his material from north Baffin Bay. In the former region the 2 size groups are seen to be divided at about 3.5 mm, in the latter at about 3.2 mm. Analysis of the 2 bimodal groups showed means of 38.5 and 52.6 units (2.96 and 4.05 mm) in Davis Strait, and 36.4 and 50.6 units (2.80 and 3.90 mm) in north Baffin Bay. Tests of significance of difference between means of the 2 small and the 2 large groups of both samples showed a high degree of probability (difference between means about 3 times greater than 3 standard errors of the difference between means) of significant difference between the small groups and between the large groups in the 2 samples. That is, both the small and large groups were significantly larger in the more southerly and warmer Davis Strait than in the more northerly and colder north Baffin Bay.

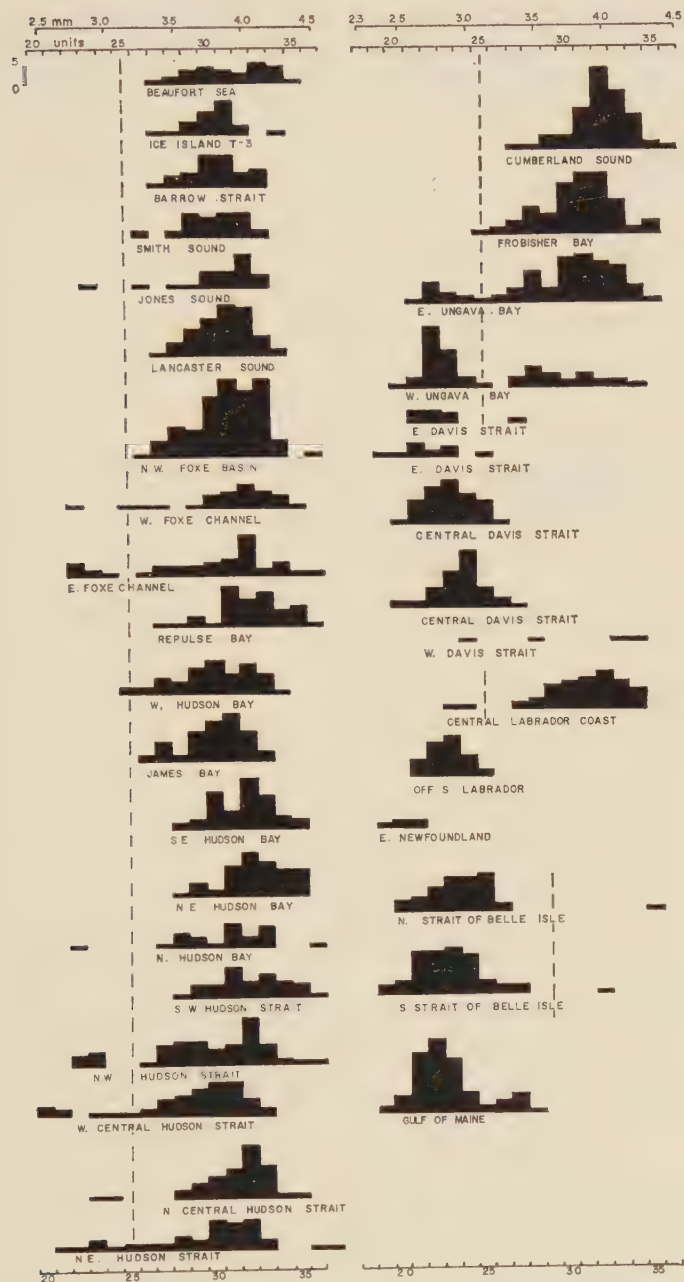


FIG. 1. Length frequency histograms of selected collections of females. Measurements are expressed in units of 0.126 mm. The vertical dashed lines show division between "large" and "small" individuals.

Of the morphological characters examined, emphasis was put on the structure of the fifth legs. From several hundred specimens examined for this character, the inner margin of the first segment of the fifth legs of 16 females between 2.4 and 4.4 mm long are shown in Fig. 3. Individuals from 2.4 to 3.2 mm long (top row in Fig. 3) and from 3.4 to 4.4 mm long (bottom row in Fig. 3) were selected as representatives of the small and large size groups respectively on the

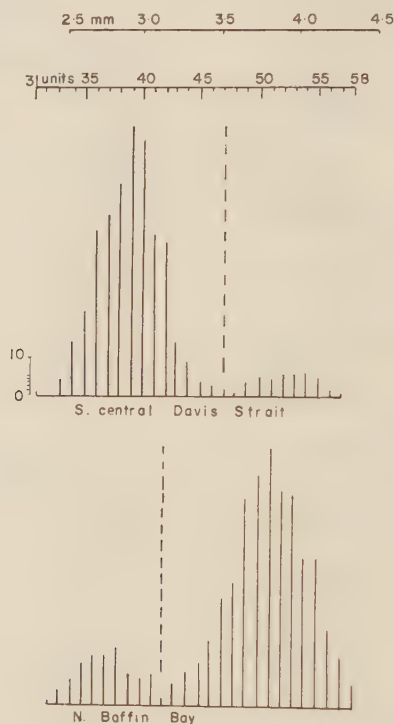


FIG. 2. Length frequency histograms of females from central Davis Strait and north Baffin Bay Godthaab stations (data from Jespersen, 1934). Lengths are given in units of 0.077 mm. The vertical dashed lines show division between "large" and "small" individuals.

basis of specimen length. Those from 3.2 to 3.4 mm long however are potentially representative of either length group on the basis of specimen length alone, depending on geographical location. Selection of illustrated representatives of this length range was made on the basis of length frequency of the whole collections from which single specimens originated, those from 3.2 to 3.4 mm in the top row of Fig. 3 being selected from collections the length frequencies of which showed

what was interpreted as the largest members of the small size group. Similarly, collections showing by their length frequency the smallest individuals of the large group were the source of individuals 3.2 to 3.4 mm long shown in the bottom row of Fig. 3.

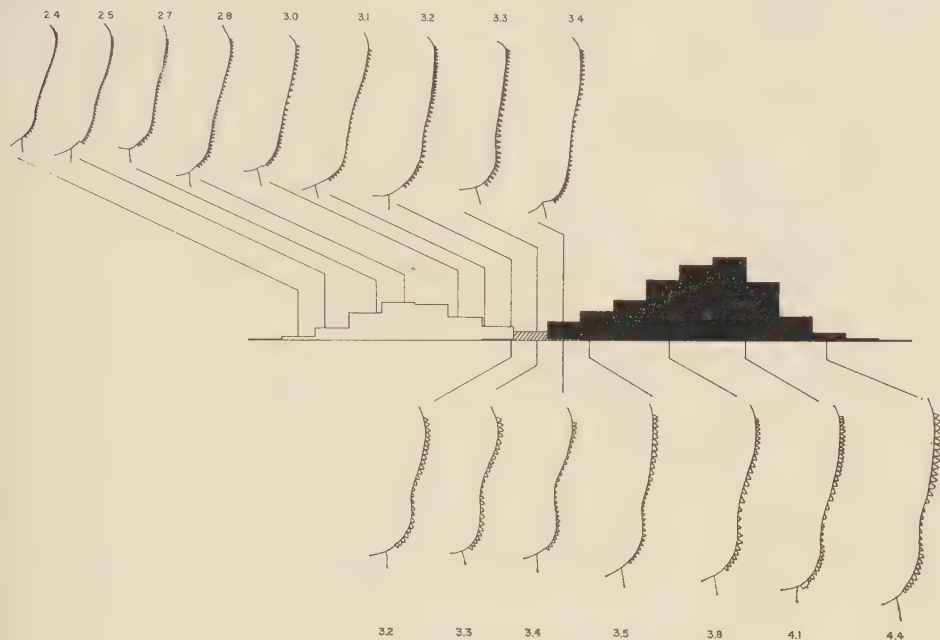


FIG. 3. First segment of the fifth legs of females.

Those of the top row resemble closely the various descriptions of *C. finmarchicus* available, in which the toothed margin is almost straight to slightly concave (Jaschnov, 1955, fig. 2; 1957, fig. 3). There is possibly a slight trend towards development of the inward curve from the smallest to the largest in this group; this trend is however by no means unvarying, for individuals up to the largest sometimes show the slightest deviation from a straight margin. Teeth tend to be relatively small and pointed. Among those shown in the bottom row, there is immediately apparent a more pronounced inward curve and larger, blunter teeth than in the small size group, with no suggestion of any trend of change in the curvature between the smallest and largest in this group. These specimens resemble the figures of *glacialis* in Jaschnov (1955), although the maximum inward curvature may be slightly less than shown by Jaschnov, being closer to the figure given by Brodsky (1959, fig. 3). Specimen length is not given for any of Jaschnov's or Brodsky's figures.

Males were few and sizes limited in available collections. Figure 4a, showing the left fifth leg of an individual 2.6 mm long, depicts *C. finmarchicus* according

to Sars (1909, pl. 3) and the description by Jaschnov (1955). Both this figure and that of Sars show the last segment of the endopodite reaching about two-thirds of the way along the penultimate segment of the exopodite, while in Jaschnov's figure the endopodite reaches almost to the distal end of the sub-terminal exopodite segment. Brodsky (1959) illustrates a structure intermediate

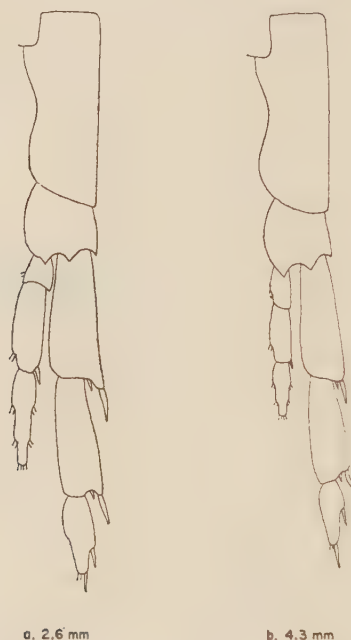


FIG. 4. Left fifth legs of males.

to Sars and Jaschnov. Figure 4b, the fifth left leg of a male 4.3 mm long, agrees with Jaschnov's description of *glacialis* but differs from his figure in having the last endopodite segment reaching about two-fifths of the way along the second last endopodite segment. There is obviously considerable variation in these structures, insufficient however to prevent inclusion of the specimens illustrated in *finmarchicus* (the smaller one) and in *glacialis* (the larger one).

Measurements were made of the ratio of body width to length throughout the size range. Figure 5 shows results of measurements made on 217 females from 2.4 to 4.5 mm long. The top solid line represents a width to length ratio of 1:3.5, the bottom solid line a ratio of 1:3.0, the dashed lines the approximate means of the 2 groups, the small one shown as open circles, the large one as dark circles. Most individuals (all but 2) of the small group fall within the range given by Jaschnov for *finmarchicus* (1:3 to 1:3.5). Most of the large group however also fall between 1:3 and 1:3.5 (Jaschnov's *glacialis* was given as 1:2.7 to 1:3); more than in the small group however are relatively broader, and about 20% of

these measured show a width-length ratio of less than 1:3. There is in general a relative widening of the cephalothorax with increase in its length in both groups, but among the largest of the small group there appears to be on the average a greater relative width than among the smallest of the large group. As far as practicable differentiation between the 2 groups is concerned, this criterion appears to have statistical value only, and not to serve as a basis for placing individual copepods within one group or the other.

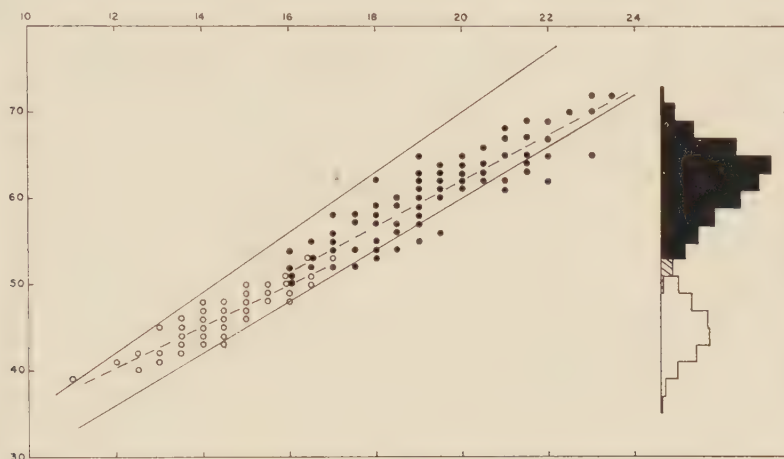


FIG. 5. Ratio of body width to length in units of 0.063 mm. The upper line shows a width to length ratio of 1:3.5, the lower line a ratio of 1:3.0.

Jaschnov (1957) presented data on the number of spines on the outer edge of the terminal endopodite segment of the fifth legs of females. Of 100 specimens of *finmarchicus*, 71% were reported to have only one spine, 25% 2 spines and 4% one and two (on different legs). Of 100 *glacialis*, 41% had one spine, 39% had 2 spines and 20% had 1 and 2 spines. Seventy specimens from both size groups were investigated here in this way, and data are given in Table I. In all, 70% have only 1 spine per leg, and there appears to be a clear and regular trend towards

TABLE I. Number of spines on the outer edge of the last endopodite segment of the fifth leg of females.

Cephalothoracic length (units)	Individuals with 1 spine	Individuals with 2 spines
20	8	2
22	8	2
25	7	3
27	8	2
30	6	4
32	7	3
35	5	5

fewer individuals with only 1 spine among the larger animals, varying from the order of 80% in the smallest to the order of 50% in the largest. There appears to be no sharp distinction on this basis between the two.

On the basis of size and structural differences discussed above, it is concluded that there is a consistent distinction between members of the so-called large and small size groups of *Calanus* in the area considered here; size difference serves in the majority of instances to distinguish members of one from the other, but within the size range shown to be common to both groups, in different parts of their range, individuals may be placed with reasonable certainty into either one or the other of the groups on the basis of fifth leg structure. Because of the degree and apparent consistency of this distinction, it is suggested that the large group be referred to *Calanus glacialis* Jaschnov, the small group to *Calanus finmarchicus* (Gunnerus), and that former records of *C. finmarchicus* from much of the arctic area of North America be considered as referring to *C. glacialis*.

ZOOGEOGRAPHICAL FEATURES

Locations of collections used in this work are shown in Fig. 6 as circles. Squares in the figure represent some of the Godthaab stations reported by Jespersen (1934) and other collections (Currie, 1918; Willey, 1919). Arrows indicate principal water movements. Dark circles are stations where only *glacialis* were found, and show exclusive occurrence of this species in the Beaufort and Polar Seas, among the islands of the arctic archipelago east to Smith Sound and eastern Lancaster Sound, south to southwest Foxe Basin, Hudson and James Bays, and along east Baffin Island south to Frobisher Bay. Half-dark and quarter-dark circles represent mixed collections of both *glacialis* and *finmarchicus* which extend from south Foxe Basin and north Hudson Bay through Hudson Strait and Ungava Bay, and from as far north as eastern Jones Sound southward to at least the Gulf of Maine. Quarter-dark and half-dark squares symbolize the same ratios of the 2 species, and show mixed populations as far north as Smith Sound with, at least in the north, relatively greater numbers of *glacialis* in west than in east Baffin Bay. White symbols represent occurrence of *finmarchicus* only, and are limited largely to central Davis Strait, being found also in the Gulf of St. Lawrence, south of Newfoundland and Nova Scotia and in the Gulf of Maine. Occurrence of *glacialis* south of Newfoundland and Nova Scotia (from Willey, 1919) may be seen at the northern colder stations only, locations farther offshore showing *finmarchicus* only. Collections considered from the southernmost part of the area treated here are few and do not necessarily show the southernmost limit of *glacialis*. It does seem probable however that south of Labrador *glacialis* is comparatively rare, and that its occurrence may be limited by the southernmost extension of subarctic water. Precise definition of its southern range would be of great value.

Occurrence of the 2 species obviously coincides to a considerable degree with water movements. Unmixed polar water flowing southward and southeastward



FIG. 6. Distribution of *Calanus glacialis* and *C. finmarchicus* in northern North America. Circles indicate collections first reported here, squares collections described by others (mostly Jespersen, 1934). Arrows denote principal water movements.

from the Arctic Ocean appears to support exclusively *glacialis* as unmixed Atlantic water to the south evidently contains only *finmarchicus*. The most northerly and westerly representatives of *finmarchicus* were found in south Smith Sound, east Jones Sound, south Foxe Basin and immediately south of Southampton Island, all of which receive warm currents with Atlantic influence. In Baffin Bay and Davis Strait, except at the strongly arctic near-shore station off south Greenland, Jespersen's data show a definite preponderance of *glacialis* on the arctic Canadian side, of *finmarchicus* on the more mixed Greenland side. It appears that exclusive occurrence of each of the 2 species, in polar and in boreal water, is separated by a combination of the 2 in the intermediate subarctic or mixed polar and Atlantic water, and that the degree of mixing may possibly be reflected by the ratio of *glacialis* to *finmarchicus*.

Brodsky (1959, fig. 5) shows on a map the general distribution of *C. glacialis* and *C. finmarchicus*, along with other species of *Calanus*. The line separating the 2 forms falls generally within the subarctic region as shown by Dunbar (1954, fig. 38), except for the northern part of the Sea of Okhotsk. Thus, except for the Sea of Okhotsk population, which may be a relict one, *glacialis* is shown by Brodsky to be a circumpolar arctic form, *finmarchicus* s.s. to be adjacent to it in the North Atlantic. While Brodsky did not show any region of mixture of the 2 forms, it is possible that the subarctic area may be defined, at least north of the Atlantic, by the occurrence of *Calanus glacialis* and *Calanus finmarchicus* together.

THE RELATION BETWEEN LATITUDE AND SIZE

The condition of poikilothermous animals in higher latitudes reaching greater size and greater age, as a result of slower growth, is widely known, and has been a readily available explanation for the presence of large *finmarchicus* in cold waters, small ones in warm waters. Marshall and Orr (1957), for example, concluded of *finmarchicus* that, apart from size variation associated with time of development within a year, the largest individuals were found in the coldest, the smallest in the warmest part of the range.

Considering the "small form" (*finmarchicus*), by itself, Clarke and Zinn (1937) found off Woods Hole a length range over the year of about 2.10 to 3.10 mm, and a range of mean values of about 2.30 to 2.75 mm, the greatest length occurring in March, the smallest in summer. Similar figures, although with variations in the times of maximum and minimum lengths, come from various workers in the British Isles. In the present material, the mean length of the Gulf of Maine sample is 2.80 mm (range 2.38 to 3.13 mm); the collection was made in April, probably near the time of greatest length. Means of 2.86 and 2.94 mm from the Strait of Belle Isle (range 2.38 to 3.38 mm) were obtained from late September collections. Similar means (2.86 and 2.94 mm) were recorded from southeast Davis Strait. In central Davis Strait a mean of 2.96 mm (range 2.50 to 3.38 mm) was found near mid-August, and a still larger size was found in the Godthaab material (Jespersen, 1934) from near the same location in mid-June, where the

mean was 3.08 mm (range 2.54 to 3.39 mm). Farther into arctic waters, mean values are lower: Ungava Bay, 2.86 mm (range 2.63 to 3.13 mm), and 2.84 mm (range 2.50 to 3.13 mm); north Baffin Bay (from Jespersen, 1934), mean 2.80 mm (range 2.46 to 3.23 mm). Overall range of mean lengths considered here is 0.33 mm, a figure smaller than the 0.45 mm total yearly range of means from off Woods Hole. But this overall range is much greater than the maximum difference (0.12 mm) between mid-June and mid-August apparent in central Davis Strait, and probably considerably greater than the seasonal range at any one location in the area considered here. There is therefore evidence to indicate an increase in length from the south at least part way to the northern limit in *finmarchicus*, and that maximum size is reached in the intermediate portion and not necessarily in the northernmost (or most arctic) part of the range.

Something similar is suggested from the available data on the large *glacialis*. The greatest mean length (3.98 mm; maximum 4.66 mm) was found in what may be called the intermediate area of Foxe Basin, Hudson Strait and north Hudson Bay, with smaller individuals taken in the Arctic Ocean and high-arctic archipelago (mean 3.83 mm; maximum 4.28 mm) and in Baffin Bay, Davis Strait and more southerly regions (mean 3.87 mm; maximum 4.41 mm). These data are in keeping with Jespersen's (1934) maximum length west of Greenland of less than 4.5 mm and Huntsman's (1919) maximum length in the Newfoundland-Nova Scotia region of about 4.4 mm. The greatest length found in a small sample, taken in winter, from the Gulf of Maine was only 3.59 mm, the mean length of 10 individuals 3.39 mm. It may be pointed out too that north European and Asian collections (Jaschnov, 1955) show the largest individuals from the Barents and White Seas, with smaller specimens reported from the more arctic Polar, Kara and Greenland Seas, as well as in the more southerly Seas of Okhotsk and Japan.

There appears to be in both *finmarchicus* and *glacialis* variation in length latitudinally over their range. The smallest individuals develop in the southern (warmest) parts, the largest intermediate to the north-south limits of distribution, and, it is suggested, smaller sized individuals towards the northern (coldest) extremities. While the ranges of both are in large part separate, there is an appreciably large area of overlap in which the largest individuals of both appear. Data suggest however that the largest individuals of both *finmarchicus* and *glacialis* do not develop together, but rather that the largest *glacialis* occur farther north (in colder, more arctic water) than the largest *finmarchicus*. This, if correct, would imply that the coldest waters do not necessarily produce the largest individuals of either species, and that both have optimum and slightly differing environmental conditions under which maximum size is attained. It seems from this that the tendency toward development of greater size with decreasing temperature may be checked in the lowest temperature range by a factor or factors which in some way inhibit further size increase. The possibility of this being food supply can be only conjecture with our present knowledge of high arctic conditions. It may be stated however that available food for *C. glacialis* in the northern and western parts of the arctic archipelago appears to be in far shorter supply than in the regions of Foxe Basin, North Hudson Bay and Hudson

Strait, or off east Baffin Island. Increase in size achieved with decreasing temperature may prevail as long as food supply remains adequate. With further decrease in temperature (that is, farther into the arctic), reduced food supply may inhibit additional increase in size and possibly result in a decrease in maximum size attained.

YOUNGER STAGES

So far, separation of *glacialis* and *finmarchicus* has been made primarily between adult females. In adult males and in stage V copepodites, fifth leg structure appears to be a valid criterion of difference between the two, and in the latter at least a clear length distinction has been shown. In collections such as Digby's (1954) from East Greenland (referred to *C. finmarchicus* only), 2 length groups are apparent in stage IV, suggesting, as in stages V and VI from the same area, the presence of both species. No structural differences however have been shown between the 2 size groups in this stage. There has not been shown any clear indication of bimodality in length distribution of stages younger than stage IV. However, comparison of Digby's East Greenland data, which from length ranges may have included both species although all were called *finmarchicus*, and Grainger's (1959) Foxe Basin data, which evidently included only *glacialis*, suggests a possible length difference in the younger stages. Similar maximum lengths are shown in all stages from VI to II, and minimum lengths in stages VI and IV in Foxe Basin are almost identical with minimum lengths of the large size group in the same stages in East Greenland. Minimum lengths in stages III and II in Foxe Basin however fall close to the median lengths of the same stages in East Greenland. Larger mean lengths therefore for stages II and III were found in Foxe Basin than in Greenland, the Foxe Basin length range approximating the upper half of the length range in both stages in East Greenland. At a much younger level, the possibility of distinguishing between the eggs of *finmarchicus* and *glacialis* comes from observations of Marshall *et al.* (1953) who reported a form from Trømso, Norway, which according to Jaschnov (1957) may be *C. glacialis*.

ACKNOWLEDGMENTS

The author is grateful to the following for providing specimens: Dr N. J. Campbell, Mr W. B. Bailey, Mr A. E. Collin and their associates for plankton collections from H.M.C.S. (later C.G.S.) *Labrador* from Davis Strait, Baffin Bay, Hudson Strait, Foxe Basin and among the islands of the arctic archipelago; Mr Collin for plankton from Ice Island T-3; Mr A. H. Lawrie for collections from the *Cancolim II* from the Beaufort Sea; Dr W. F. Black for material from Pelly Bay; Mr H. J. Squires for plankton from the Newfoundland area; Dr R. J. Conover for specimens from the Gulf of Maine; and Dr D. E. Sergeant for material from Newfoundland.

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Comparative Osteology of Representative Salmonid Fishes, with Particular Reference to the Grayling (*Thymallus arcticus*) and its Phylogeny^{1, 2}

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ABSTRACT

The purpose of this study is to describe the morphology, particularly the osteology, of the grayling (*Thymallus arcticus*), in relation to that of the other salmonid fishes, in order to assess the phylogenetic position of the grayling and to synthesize the natural classification of the Salmonidae.

Fresh and preserved material of 33 species in 9 genera of Salmonidae were studied. The study materials included dried whole skeletons from fresh fishes, stained bones of preserved specimens, and cross sections of larval stages. Effort was made to eliminate bias due to ontogenetic and sexual differences.

The Salmonidae are soft-rayed teleost fishes belonging to the suborder Salmonoidei of the generalized order Clupeiformes (Isospondyli). Prior classifications of the salmonids have arranged them into one, two, or three families. As herein visualized, the family Salmonidae contains those salmonoid fishes that have three upturned caudal vertebrae. They are divided into three subfamilies: Salmoninae, the trouts and salmons, with an orbitosphenoid bone and a suprapreopercular bone, a basibranchial plate, teeth on the maxilla, no dermosphenotic bone, and parietals separate at the midline; Thymallinae, the graylings, with no orbitosphenoid, suprapreopercle or basibranchial plate, a dermosphenotic bone, teeth on the maxilla, and parietals meeting at the midline; and Coregoninae, with orbitosphenoid and dermosphenotic bones, no suprapreopercle, no teeth on the maxilla, and parietals meeting at the midline.

The grayling possesses only two invariable morphological differences from other salmonids. These are the absence of an orbitosphenoid bone and the presence of seventeen or more dorsal fin rays. In other characters, there is overlap with one or the other subfamilies.

Three osteological characteristics are thought to be more fundamental than the others: the toothless maxilla in the Coregoninae, the lack of an orbitosphenoid in the Thymallinae, and the separation of the parietals by the supraoccipital in the Salmoninae. Each character is distinctive for only one subfamily, it being common to the other two. The complete bony and cartilaginous skeletal system of the grayling is illustrated, as are many osteological features of the trouts and whitefishes.

Within the subfamily Salmoninae, 5 genera (*Brachymystax*, *Hucho*, *Salvelinus*, *Salmo*, and *Oncorhynchus*) are recognized and defined. The Thymallinae consists of a single genus *Thymallus* with 4 species. Three genera of Coregoninae are recognized: *Prosopium*, *Coregonus*, and *Stenodus*. The discovery that *Prosopium* has a basibranchial plate, taken together with previously known characters, justifies recognition of generic rank for this group. The group commonly ranked as a genus *Leucichthys* does not display enough difference to warrant such segregation and is synonymized with the genus *Coregonus*. *Stenodus* is found to have distinctive characters not heretofore noted and may rank as a genus separable from but related to *Coregonus*.

¹Received for publication October 4, 1960.

²Based on a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan, 1958.

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INTRODUCTION

THE GRAYLINGS are soft rayed teleost fishes belonging to the suborder Salmonoidei of the generalized order Clupeiformes (Isospondyli). They are most closely allied to the trouts and whitefishes, and some authors (Boulenger, 1895; Regan, 1914) have assigned all three groups to the family Salmonidae. Others (Jordan and Evermann, 1896; Tchernavin, 1923; Berg, 1940, 1955) have placed the graylings in a separate family, the Thymallidae. Since the literature is incomplete regarding the osteology of the grayling, this study was undertaken to advance our knowledge of fish morphology. Comparisons with other salmonoid fishes were made in order to clarify the phylogenetic position of the grayling and to place the classification of the Salmonidae on a firmer foundation.

Berg (1940) listed 11 families among the Salmonoidei, but revisions by Chapman (Plecoglossidae, 1941a; Osmeridae, 1941b; Argentinidae, 1942; Microstomidae, 1948) and recent lumping of several bathypelagic families from the suborders Opisthoproctoidei and Salmonoidei into the Argentinidae (Hubbs, 1953) have reduced this number to about seven. The Salmonoidei are characterized by the presence, usually, of an adipose fin, ribs inserted on autogenous parapophyses, the neural and haemal arches of the caudal fin skeleton are laterally compressed, and oviducts absent or incomplete (Regan, 1913; Gosline, 1960). The salmonines (trouts), coregonines (whitefishes), and thymallines (graylings) are separable from the other salmonoid fishes by the three upturned vertebrae in the caudal fin (Regan, 1914). They have been variously placed in one, two or three families, but that the three groups constitute a monophyletic assemblage seems generally agreed. This assemblage is here regarded as a family, Salmonidae, and the three included groups are treated as subfamilies: trouts, Salmoninae; whitefishes, Coregoninae; and graylings, Thymallinae.

The graylings consist of a single genus *Thymallus* composed of 4 species, as revised by Svetovidov (1936). *Thymallus brevirostris* Kessler (*Phylogeophyra* Boulenger) has larger teeth than the other 3 species and the articulation of the lower jaw is situated behind the posterior margin of the eye. It has a very restricted range in northwest Mongolia. *Thymallus thymallus* (Linnaeus) has less well developed teeth than does *T. arcticus* and the maxilla does not extend beyond the anterior margin of the eye. It is found in the British Isles and across northern and central Europe. *Thymallus nigrescens* Dorogostajskij is similar to *T. arcticus* but it has more gill rakers (26 to 33 as compared with 14 to 22 in *T. arcticus*). It is restricted to Lake Kosogol in Mongolia (Svetovidov, 1936). *Thymallus arcticus* has the widest distribution of the four, occurring from western Siberia across northern Asia into North America. In North America there once lived 3 (possibly 4) isolated stocks of *Thymallis arcticus*. The most widely distributed of these, named *Thymallus signifer* by Richardson (1823), occurs in Alaska and northern Canada. *Thymallus montanus* (Milner, 1874) was described from mountain streams of the upper Missouri drainage. *Thymallus tricolor* (Cope, 1865) a now extinct geographic stock, was once abundant in the streams of northern Michigan along the upper Great Lakes. A possible fourth colony

may have been native to Lake Ontario, whence came two museum specimens, the types of *Thymallus ontariensis* Valenciennes (see Jordan and Evermann, 1896: 518; Bertin, 1940: 306).

American workers have classified these several stocks variously as distinct species, as subspecies of a single species, or as comprising two species, one with two subspecies. Walters (1953, 1955) treated the American grayling, *Thymallus signifer*, as conspecific with the Asiatic species, *Thymallus arcticus* (Pallas), and relegated the American forms to subspecific status without giving characters for the latter. Whether or not the 4 geographic stocks of American graylings are sufficiently distinct to merit separation into subspecies is uncertain. A careful comparison of the forms is needed, but this is beyond the scope of the present inquiry.

Both the European grayling, *Thymallus thymallus* (Linnaeus), 1758, and the eastern Siberian form, *Thymallus arcticus* (Pallas), 1793, were originally described in *Salmo*. Richardson, in describing the North American form *signifer* (1823), placed it in the genus *Coregonus*. *Thymallus* (proposed by Cuvier, 1829) was separated from *Salmo* on the basis of the small mouth and teeth, less deeply cleft jaws, long and high dorsal fin, and larger scales. The coregonine fishes were separated from the salmonine fishes by Cope (1871, 1872) chiefly because the parietal bones meet at the midline in the coregonines, and are separated by the supraoccipital bone in the salmonines. Gill (1893, 1895) disputed the work of Cope and stated (incorrectly) that in the coregonines the parietals are also separated by the supraoccipital. This left *Thymallus* as the only genus with parietals in contact, and as a result, Gill created the family Thymallidae, using the long dorsal fin and the presence of epipleural spines on the anterior ribs as supporting evidence for the action. The coregonines were relegated to subfamily status within the Salmonidae. Boulenger (1895) called attention to Gill's erroneous observation on the parietal separation in the whitefishes. He pointed out that all salmonoid fishes have epipleural spines and that the development of the dorsal fin is too trivial to be used as a family character. Consequently he saw no sound evidence for separating either the thymallines or the coregonines from the Salmonidae. Jordan and Evermann (1896) retained Gill's classification and used the same diagnostic characters. In Regan's classification (1914) the Salmonidae was divided into two subfamilies, the Salmoninae, with stronger dentition, separated parietals and smaller scales, and the Coregoninae. *Thymallus* was assigned to the Coregoninae, because it has weak dentition, parietals meeting at the midline, and large scales. Kendall (1935: 8) stated that *Thymallus* is not a link between the coregonines and salmonines and that the ensemble of characters of both *Thymallus* and *Stenodus* is more than generically distinct. Tchernavin (1923; 1939) recognized the graylings as a separate family, closely related to the Salmonidae, but without an orbitosphenoid bone. He further distinguished the Thymallidae from the Osmeridae by the absence of teeth on the mesopterygoid bone. In the recent classification by Berg (1940, 1955) the graylings were again placed in a separate family, Thymallidae, because of the lack of an orbitosphenoid, the presence of three tabulars on each side, a hypethmoid bone, two supraorbitals,

and a long dorsal fin. The salmonines and coregonines were ranked as sub-families of the Salmonidae.

An abundant literature has appeared on the embryology and osteology of the Salmoninae, particularly *Salmo salar* Linnaeus and *Salmo trutta* Linnaeus. The early works date from Parker (1873), but the more recent osteological papers by de Beer (1927, 1937), Gregory (1933), Saunderson (1935), Holmgren and Stensiö (1936), and Tchernavin (1937, 1938a, 1938b) were particularly useful in this study. The coregonine fishes have received less extensive morphological study, although Price's (1934) work on the embryology of *Coregonus clupeaformis* (Mitchill) and Berg's (1940: 232–238) osteological material on *Coregonus lavaretus* (Linnaeus) and *Stenodus leucichthys* (Güldenstädt) have been helpful.

No complete account of the osteology of the grayling appears in the literature, although a number of diagnostic characters have been mentioned in conjunction with studies on other salmonoid fishes. This deficiency has resulted in some discrepancies and disagreement in regard to the morphology of the grayling and to its phylogenetic position.

The primary object of this work is an attempt to bridge the gap in our knowledge of the salmonoid fishes by presenting a description of the osteology of the grayling, *Thymallus arcticus* (Pallas). In addition, the phylogenetic position of the grayling is investigated through comparison with other salmonids and the classification of the Salmonidae is assessed.

At the taxonomic level at which this work was conducted, the skeleton appears to present the greatest promise for reliable comparison, and it has been stated (Tchernavin, 1937: 237) that "osteology offers a fairly safe guide to the natural arrangement of fishes." However, developmental stages and other morphological aspects have been studied to some extent.

ACKNOWLEDGMENTS

A number of people gave substantial assistance in this work. I wish to express my appreciation to Drs David C. Chandler, Elzada U. Clover, George C. Rinker, and Alfred H. Stockard. I am especially grateful to Dr Reeve M. Bailey, Curator of Fishes in the Museum of Zoology, who gave much of his time and made numerous recommendations throughout the progress of the research.

I am indebted to a number of people who assisted in obtaining fresh specimens for this study: Drs Stanford H. Smith and Alfred M. Beeton, United States Fish and Wildlife Service, for the ciscoes; Dr Paul H. Eschmeyer, Institute for Fisheries Research, Michigan Department of Conservation, for the lake trout and brook trout; Dr C. J. D. Brown, Montana State College and Mr A. E. Tangen, Montana Department of Fish and Game, for the grayling; Dr Norman Wilimovsky, United States Fish and Wildlife Service, for the salmon; and Mr N. S. Novakowski, Canada Department of Northern Affairs and Natural Resources, for the inconnu (*Stenodus*).

Dr Andrew Starrett assisted in the translation of Russian papers. Many of the illustrations would not have been possible without the help and advice of

Mrs. Elizabeth Anthony, Division of Fishes of the Museum of Zoology. The plates of the chondrocrania, as well as many helpful ideas on the other illustrations are a credit to her. My wife, Phyllis Norden, gave much of her time in typing, illustrating, and cooperating throughout the course of the study.

MATERIALS, METHODS AND TERMINOLOGY

MATERIALS

The data on *Thymallus arcticus* were obtained from three sources: developmental stages, preserved specimens, and fresh adult fish. Developmental stages were collected from hatchery material by Mr A. E. Tangen of the Montana Department of Fish and Game. Specimens were collected at the time of hatching (total length 12.0 mm) and at 3-day intervals thereafter for 2 months (total length 34.5 mm). Twenty-two specimens (standard length 27.0 to 128.5 mm) were obtained from preserved material (UMMZ 167092, 169572, 169573, 169574, 169575) in the University of Michigan Museum of Zoology. These came from fish hatcheries in South Dakota, Wyoming, and Montana, or were collected in Alaska. Twelve mature adults in spawning condition (standard lengths 275.0 to 335.0 mm) were collected from Red Rock Creek, Beaverhead County, Montana by Dr C. J. D. Brown of Montana State College. These were frozen and were used for fresh osteological preparations (UMMZ 172465-S).

A substantial amount of fresh material was available for comparative study. When this was inadequate, preserved museum specimens were employed. Tables I, II and III itemize the material used, some merely for X-rays, some for extended study.

TABLE I. Specimens of Coregoninae used in the study.

Species	Number of specimens	Standard length	UMMZ number
	<i>no.</i>	<i>mm</i>	<i>No.</i>
<i>Coregonus alpenae</i> (Koelz)	2	120 to 140	172475-S
<i>Coregonus artedii</i> LeSueur	42	25 to 267	95649, 95650, 145300, 172466-S, 172467-S, 172471-S, 172472-S, 172473-S, 172474-S, 172480-S
<i>Coregonus clupeaformis</i> (Mitchill)	17	28 to 325	54314, 75323, 75324, 75327, 75332 to 75335, 81555, 162159
<i>Coregonus hoyi</i> (Gill)	13	75 to 205	52930, 54349, 172479-S
<i>Coregonus kiyi</i> (Koelz)	10	132 to 218	59415, 59438, 59439, 172477-S
<i>Coregonus nasus</i> (Pallas)	1	375	
<i>Coregonus reighardi</i> (Koelz)	4	191 to 211	172476-S
<i>Coregonus sardinella</i> Valenciennes	2	216 to 239	
<i>Prosopium abyssicola</i> (Snyder)	2	120 to 140	141811
<i>Prosopium coulteri</i> (Eigenmann and Eigenmann)	18	59 to 110	167953, 167954, 169058-S
<i>Prosopium cylindraceum</i> (Pallas)	12	31 to 297	52880, 59702, 59732, 59804, 68929, 141761, 167963
<i>Prosopium gemmiferum</i> (Snyder)	10	149 to 167	141809, 156788
<i>Prosopium spilonotus</i> (Snyder)	2	151 to 157	162330
<i>Prosopium williamsoni</i> (Girard)	6	53 to 147	140241, 161844
<i>Stenodus leucichthys</i> (Güldenstädt)	8	474 to 630	161995, 162455, 172387-S

TABLE II. Specimens of Salmoninae used in the study.

Species	Number of specimens	Standard length	UMMZ number
	<i>no.</i>	<i>mm</i>	<i>No.</i>
<i>Brachymystax lenok</i> (Pallas)	1	132	172490
<i>Hucho hucho</i> (Linnaeus)	1	493	177294
<i>Hucho perryi</i> (Brevoort)	1	284	172493
<i>Oncorhynchus gorbusha</i> (Walbaum)	3	62	147432, 172444-S
		(2 adult heads)	
<i>Oncorhynchus keta</i> (Walbaum)	10	45 to 176	106275, 141105, 172452-S
<i>Oncorhynchus kisutch</i> (Walbaum)	5	38 to 58	93847
		(1 adult head)	
<i>Oncorhynchus masou</i> (Brevoort)	2	112 to 125	
<i>Oncorhynchus nerka</i> (Walbaum)	17	70 to 252	117877, 144805, 166742, 167457
		(7 adult heads)	172443-S, 172453-S, 172454-S
<i>Oncorhynchus tshawytscha</i> (Walbaum)	12	36 to 258	93867, 143188, 146364, 146365,
		(1 adult head)	147328
<i>Salmo clarki</i> Richardson	5	167 to 239	136872, 167463
<i>Salmo gairdneri</i> Richardson	16	44 to 273	61837, 127601, 171042-S,
			172468-S, 172469-S
<i>Salmo ohridanus</i> Steindachner	1	234	177293
<i>Salmo salar</i> Linnaeus	10	49 to 155	126538, 141019, 145562
<i>Salmo trutta</i> Linnaeus	18	19 to 413	1245553, 130641, 172470-S
<i>Salvelinus fontinalis</i> (Mitchill)	32	29 to 266	69641, 85467, 172462-S
<i>Salvelinus malma</i> (Walbaum)	3	(3 adult heads)	172458-S
<i>Salvelinus namaycush</i> (Walbaum)	32	22 to 653	81645, 162155, 172463-S,
			172464-S, 172481-S to 172486-S

TABLE III. Other salmonoids used in the study.

Species	Number of specimens	Standard length	UMMZ number
	<i>no.</i>	<i>mm</i>	<i>No.</i>
OSMERIDAE			
<i>Allosmerus attenuatus</i> (Lockington)	4	46 to 75	60911, 93883
<i>Hypomesus olidus</i> (Pallas)	2	77 to 83	61245
<i>Hypomesus pretiosus</i> (Girard)	2	102 to 109	93887
<i>Osmerus mordax</i> (Mitchill)	23	42 to 187	72242, 172478-S
<i>Spirinchus thaleichthys</i> (Ayres)	2	80 to 97	60919
ARGENTINIDAE			
<i>Argentina sialis</i> Gilbert	2	88 to 103	94697, 94698
<i>Argentina silus</i> Ascanius	1	93	147278
PLECOGLOSSIDAE			
<i>Plecoglossus altivelis</i> Temminck and Schlegel	1	281	169000

Some observations were made on the Elopidae, Osmeridae, Argentinidae, and Plecoglossidae, especially to check statements made by other workers. Except for *Osmerus mordax*, all were based on preserved material.

All study material is preserved in the Museum of Zoology of the University of Michigan (UMMZ).

METHODS

Cross sections were made of the early stages (12 to 30 mm in total length) for *Thymallus arcticus*, *Coregonus artedii* and *Salmo trutta*. These were fixed in either Bouin's fluid or 10% formalin and stained with Harris's hematoxylin and eosin (Guyer, 1953). Preserved specimens were cleared in a solution of KOH and stained with alizarin red S for bone, or toluidine blue for cartilage, following the method prescribed by Evans (1948). Dried whole skeletons were prepared from fresh material by use of dermestid beetle larvae. Since cartilage occupies an important part of the skeleton of salmonoid fishes, dried preparations were unsuitable for some work. Therefore, some specimens were disarticulated for study after immersing the fresh fish briefly in hot water to loosen the flesh. The bones were later stained with alizarin red S and preserved in alcohol or glycerine. Gross anatomical dissections were made on both preserved and fresh material before skeletons were prepared. Where available specimens were few, additional vertebral counts were obtained from X-ray negatives of preserved specimens. In contrasting the osteology of different species, either specimens of comparable lengths or an equivalent stage of sexual maturity were employed.

In general, measurements and counts are adapted from Hubbs and Lagler (1947). All measurements were made in millimeters with dividers. The *total length* is the greatest dimension, in a straight line, from the anterior tip of the head to the posterior tip of the caudal fin. This measurement was used for developmental stages, before the vertebrae were ossified and while the caudal fin was heterocercal. The *standard length* is the greatest dimension, in a straight line, from the anterior tip of the upper lip to the hidden base of the caudal fin rays. All *rays* (rudimentary and principal) were counted in the dorsal, anal, and paired fins. In the dorsal and anal fins, the last ray is considered double at the base and is counted as one. The caudal fin ray count is the number of branched rays, plus two. The count of *gill rakers* is that of the first arch, with rudimentary rakers included. Unless otherwise stated, the *branchiostegal rays* counted includes all the branchiostegals on the left side. Three rays are usually borne on the epihyal and the remainder on the ceratohyal. The *pyloric caeca* include the tips of all the finger-like projections at the junction of the stomach and intestine. In making the count of *vertebrae*, each centrum was counted as one if it was separated on either side by a definite suture. Thus, the last three upturned vertebrae were counted as three. The precaudal vertebrae include all those that do not have a well-developed haemal spine. The rib, epineural, and epi-pleural count is an enumeration of all of these structures that are wholly or partially ossified.

Observations and measurements of skeletal elements, ova, and developmental stages were made with dividers under a dissecting binocular microscope. Illustrations were made from photographs and from drawings, using a compound microscope with a camera lucida.

TERMINOLOGY

The osteological terminology adopted is that most commonly accepted. Unless otherwise stated it agrees with Harrington (1955) for the skull, Stokely (1952) for the vertebral column, Starks (1930) for the pectoral girdle, and Regan (1910) for the caudal fin.

Abbreviations, definitions and synonyms of skeletal elements are as follows:

- A. Angular, *os angulare* (dermarticular, Goodrich, 1930; articular, Gregory, 1933; de Beer, 1937; Berg, 1940). A pair of jaw bones which are both endochondral and intramembranous in origin, and which fit into the triangular notch of the dentaries, anteriorly and articulate posteriorly with the quadrates.
- AC. Actinost, *os actinostum* (radial, Goodrich, 1930; Berg, 1940; Dineen and Stokely, 1954). The four small endochondral bones of each pectoral girdle which articulate proximally with the scapulae and distally with the fin rays.
- AFR. Anal fin ray (Iepidotrichia, Goodrich, 1930). The dermal rays, both rudimentary and principal, of the anal fin.
- BB. Basibranchial, *os basibranchialium* (anterior copula, Tchernavin, 1938b; copulae, Ramaswami, 1952a, 1952b). A series of 4 unpaired endochondral bones forming the floor of the oral cavity. The first articulates anteriorly with the cartilaginous basihyal and the fourth articulates posteriorly with the cartilaginous basibranchial or posterior copula.
- BH. Basihyal, *cartilago basihyalis* (lingual cartilage, Tchernavin, 1938b; glossohyal, Ridewood, 1904a; Chapman, 1942). A single cartilaginous component forming the base of the tongue.
- BOC. Basioccipital, *os basioccipitale*. A median endochondral bone which forms the posterior floor of the cranial cavity and articulates with the first vertebra.
- BP. Basibranchial plate, *os basibranchialium plattum* (supra-copula, Tchernavin, 1938b; supra-basal, Chapman, 1941a; dental cement bone, Chapman, 1941b). A median dermal ossification covering the basibranchials and often bearing basibranchial teeth, the so-called hyoid teeth. In some species two median bones are present.
- BPTG. Basipterygium, *os basipterygium* (pelvic bones, Chapman, 1941a, 1941b). A pair of triangular endochondral bones which form the pelvic girdle.
- BR. Branchiostegal ray, *os radii branchiostegi*. A paired series of flat dermal bones which lie below the interopercles and belong to the hyoid arch. The larger, posterior 3 rays articulate with the epihyal; the remainder articulate with the ceratohyal.
- BS. Basisphenoid, *os basisphenoidum*. A small, median Y-shaped bone located in the rear of the orbit. The arms of the Y curve around the pituitary body and the leg bisects the posterior myodome and then meets the parasphenoid bone.
- C. Centrum, *os centrum*. The spool-shaped portion of the vertebra which in embryological development topographically displaces the notochord.
- CB. Ceratobranchial, *os ceratobranchialium*. A pair of long endochondral bones present in each of the five paired gill arches which articulate with the epibranchials, dorsally, and the hypobranchials, ventrally.
- CC. Coracoid, *os coracoideum*. A pair of triangular endochondral bones of the pectoral girdle which articulate with the cleithra and the scapulae.
- CH. Ceratohyal, *os ceratohyale*. The ceratohyals are a pair of flat endochondral bones which belong to the hyoid arch. They articulate anteriorly with the hypohyals and posteriorly with the epihyals. Each ceratohyal bears from 6 to 10 branchiostegal rays.

- CL. Cleithrum, *os cleithrum*. A pair of large, curved intramembranous bones which form an extensive part of the pectoral girdle.
- CM. Coronomeckelian, *os coronomeckelium* (sesamoid articular, Ridewood, 1904a; *os Meckeli*, Berg, 1940; sesamoid angular, Ramaswami, 1952a, 1952b). A pair of bones which are believed to be an intramembranous ossification on the mesial surface of the angulars.
- D. Dentary, *os dentale*. A pair of large, toothed, mixed bones of the lower jaw.
- DF. Dorsal fontanelle (temporal foramen, Berg, 1940). A pair of circular openings in the cartilaginous roof of the chondrocranium.
- DS. Dermosphenotic, *os dermosphenoticum*. The pair of small, dermal postorbital bones which bear triradiate sensory canals. They are absent in the Salmoninae.
- E. Epural, *os epurale*. Two or three, median endochondral bones which lie dorsal of the uro-neurals in the caudal fin skeleton. They are detached from the uroneurals and are believed to be modified neural spines.
- EB. Epibranchial, *os epibranchialium*. Four pairs of endochondral bones, one in each of the first four gill arches. They articulate, dorsally, with the pharyngobranchials and, ventrally, with the ceratobranchials.
- ECT. Ectopterygoid, *os ectopterygoideum* (pterygoid, Chapman, 1941a, 1941b, 1942; Dineen and Stokely, 1954). A pair of thin, splint-like dermal bones which lie on either side of the palate, between the palatine and quadrate bones.
- EH. Epihyal, *os epihyale*. A pair of rounded endochondral bones which belong to the hyoid arch. They articulate anteriorly with the ceratohyals and dorsally with the interhyals, and bear three pairs of branchiostegal rays.
- EHS. Expanded haemal spine. The transverse processes of the caudal vertebrae become fused and form posteroventrally directed projections. The projections belonging to the last 7 or 8 vertebrae are broad and flat, and are called expanded haemal spines.
- EN. Epineural, *os epineuralium* (epipleural, Goodrich, 1930). A series of small, paired inter-muscular bones of the axial skeleton which articulate with the anterior neural arches and point posterodorsally.
- ENS. Expanded neural spine. A series of ossifications which extend dorsad around the spinal cord and form neural arches. The posterior arches fuse to form spines which project dorso-caudally. The last 7 or 8 of the series are broad and flat, and are called expanded neural spines.
- EOC. Exoccipital, *os exoccipitale* (lateral occipital, Berg, 1940). The pair of endochondral bones which form in the posterior wall of the chondrocranium and partially surround the foramen magnum.
- EP. Epipleural, *os epipleuralium*. A paired series of short ribs which project caudally into the myocommata from the bases of the pleural ribs.
- EPO. Epiotic, *os epioticum*. A pair of endochondral bones which form in the posterodorsal surface of the chondrocranium and enclose the posterior semicircular canals.
- ES. Extrascapular, *os extrascapulare* (scalebone, Gregory, 1933; tabular, Berg, 1940; supra-temporal, Chapman, 1941a, Ramaswami, 1952b). A transverse series of from 4 to 10 dermal bones which lie behind the parietals and enclose the supratemporal sensory canal.
- F. Frontal, *os frontale*. A pair of flat, triangular dermal bones which cover most of the dorsal surface of the chondrocranium.
- FM. Foramen magnum, *foramen magnum*. The posterior opening in the chondrocranium, through which the spinal cord passes as it leaves the brain.

- H. Hypural, *os hypuralium*. A series of 7 expanded haemal spines in the caudal fin which lie ventrally of the three upturned vertebrae and the urostyle.
- HA. Haemal arch. A bridge of bone formed by an elongation of the transverse processes around the caudal artery and vein; present in a few precaudal and most caudal vertebrae.
- HB. Hypobranchial, *os hypobranchialium*. A pair of endochondral bones present in each of the first three gill arches. They articulate dorsally with the ceratobranchials and ventrally with the basibranchials.
- HE. Hypethmoid, *os hypethmoideum* (mesethmoid, Gregory, 1933; de Beer, 1937; ethmoid, Harrington, 1955). A median endochondral ossification which lies between the nasal capsules. Hypethmoid (Berg, 1940) is used to avoid confusion with the ethmoid cartilage and the supraethmoid bone.
- HH. Hypohyal, *os hypohyale*. A pair of upper and lower, cone-shaped endochondral bones of the hyoid arch that connect the ceratohyals with the median basihyal.
- HS. Haemal spine (haemal process, Berg, 1940). The posteriorly directed ventral projections formed by elongation and fusion of the transverse processes. Vertebrae which bear haemal spines are designated as caudal vertebrae.
- HY. Hyomandibular, *os hyomandibulare*. A pair of hatchet-shaped endochondral bones which suspend the lower jaw from the cranium.
- IH. Interhyal, *os interhyale*. A pair of small, cylindrical endochondral bones which connect the epihyals with the symplectic and hyomandibular bones.
- IN. Interneural, *os interneuralium* (dorsospinalia, Berg, 1940). A series of median supporting rods which lie in the muscle anterior of the dorsal fin, between the bifurcated neural spines.
- IO. Infraorbital, *os infraorbitalium* (jugal, Gregory, 1933; suborbital, Chapman, 1941a; Vladykov, 1954; Harrington, 1955). One pair of small dermal bones which lie between the lacrymals and the first pair of postorbitals.
- IOP. Interopercle, *os interoperculum*. A pair of thin, triangular dermal bones which lie below the preopercles, separating them from the subopercles.
- LA. Lacrymal, *os lacrimale* (lacrima, Allis, 1897; praeorbital, Berg, 1940; suborbital, Vladykov, 1954). A pair of small dermal bones which form the lower anterior rim of the orbits and contain the termini of the infraorbital canals.
- LP. Lingual plate, *os linguale plattum* (dermentoglossum, de Beer, 1937; supralingual bone, Tchernavin, 1938b; Vladykov, 1954; dental cement bone, Chapman 1941a, 1942). A median dermal ossification which covers the cartilaginous basihyal and bears the "tongue teeth".
- M. Maxilla, *os maxillare*. The pair of dermal bones of the upper jaw which articulate anteriorly with the premaxilla but are without a posterior articulation. They are toothed in the Salmoninae and Thymallinae but are toothless in the Coregoninae.
- MC. Meckel's cartilage, *cartilago meckeli*. Two slender rods of cartilage which extend forward from the endochondral portion of the angulars, along the mesial surface of the lower jaw to the dental symphysis.
- MES. Mesopterygoid, *os mesopterygoideum* (endopterygoid, Goodrich, 1930; Harrington, 1955; entopterygoid, Berg, 1940; Gregory, 1951). A pair of thin, triangular intramembranous bones which comprise part of the palate and the floor of the orbit.
- MSC. Mesocoracoid, *os mesocoracoideum*. A pair of curved endochondral bones which belong to the pectoral girdle and which act as braces between the cleithra, above, and the coracoids and scapulae, below.

- MET. Metapterygoid, *os metapterygoideum*. A pair of semi-circular endochondral bones which fit into a curved area formed by the quadrate, symplectic, and hyomandibular bones.
- N. Nasal, *os nasale*. A pair of small, tubular dermal bones which lie on the sides of the anterior tip of the frontals.
- NA. Neural arch. The part of a vertebra which extends dorsally from the centrum and surrounds the spinal cord.
- NS. Neural spine. The spines which are formed by the fusion of the paired neural arches and project dorsoposteriorly from the vertebral column.
- OP. Opercle, *os operculum*. A pair of large, flat intramembranous bones which cover the gills.
- OPO. Opisthotic, *os opisthoticum* (intercalary, Berg, 1940). A pair of small, conical intramembranous bones which cover the junction of the pterotic, epiotic and supraoccipital bones.
- OS. Orbitosphenoid, *os orbitosphenoidum*. A median endochondral ossification which lies between the orbits and thus forms the floor and walls of the anterior end of the cranial cavity.
- P. Parasphenoid, *os parasphenoidum*. A long, narrow, median intramembranous bone which forms the floor of the chondrocranium and extends from the vomer in front to the basioccipital, in the rear.
- PA. Parietal, *os parietale*. A pair of dorsal roofing bones which lie posteriorly of and are overlapped by the frontals.
- PAL. Palatine, *os palatinum* (autopalatine dermopalatine, Allis, 1897). A pair of splint-shaped mixed bones which lie along the margin of the palate, between the ectopterygoid and the premaxilla.
- PAP. Parapophysis, *os parapophysis* (transverse process, Stokely, 1952). Paired, ventral, transverse processes which form articular surfaces for the ribs.
- PB. Pharyngobranchial, *os pharyngobranchialium*. A pair of bones present in each of the first three gill arches. They form the most dorsal segment of the arch but only the first is attached to the parasphenoid. All three are attached to the epibranchials. Pharyngobranchials of the fourth pair are cartilaginous.
- PCL. Postcleithrum, *os postcleithrum*. Three pairs of small, scale-like dermal bones which lie in a vertical series posteriorly of the cleithra and are present in all salmonid fishes.
- PEFR. Pectoral fin ray (lepidotrichia, Goodrich, 1930). All rays of the pectoral fin, both rudimentary and principal.
- PF. Prefrontal, *os praefrontale* (preorbital, Allis, 1898; lateral ethmoid, Berg, 1940). A pair of bones in the ethmoid region which are of dual origin (dermal and cartilage), and separate the olfactory capsule from the orbit.
- PFR. Pelvic fin ray (lepidotrichia, Goodrich, 1930). All rays of the pelvic fin, both rudimentary and principal.
- PM. Premaxilla, *os praemaxillare*. A pair of curved bones which form the anterior margin of the upper jaw. They are toothed in all species of salmonid fishes, at least during some period of their life history.
- PO. Postorbital, *os postorbitalium* (circumorbitals, Ridewood, 1904a, 1904b). There are usually three pairs of thin, flat dermal bones which form the posterior rim of the orbit.
- POP. Preopercle, *os preoperculum*. A pair of curved dermal bones which lie just behind the suspensorium of the lower jaw and which partially cover the opercular bones.
- POZ. Postzygapophysis, *os postzygapophysis*. Posterior projections which are borne on the neural arches and transverse processes and which function as articulating surfaces for the vertebrae.

- PP. Pharyngeal plate, *os pharyngealium plattum*. Three pairs of small, toothed dermal plates which are found in the gill region. The first pair is borne on the third pharyngobranchials, the second pair on the fourth epibranchials, and the third pair on the fifth ceratobranchials.
- PQ. Palatoquadrate, *cartilago palatoquadrata*. A pair of narrow cartilaginous strips which separate the quadrates from the mesopterygoid and metapterygoid bones. They are considered to be a remnant of the primitive upper jaw.
- PRO. Prootic, *os prooticum*. A pair of large endochondral bones formed in the floor of the cranial cavity posterior of the orbit.
- PRZ. Prezygapophysis, *os prezygapophysis*. Anterior projections which are borne on the neural arches and transverse processes and which function as articulating surfaces for the vertebrae.
- PS. Pterospheneid, *os pterosphenoideum* (alisphenoid, Gregory, 1933; Berg, 1940; Chapman, 1941a, 1941b; pleurophenoid, de Beer, 1937). A pair of endochondral bones which lie dorsally of the prootics and posteriorly of the orbit.
- PT. Posttemporal, *os posttemporale*. A pair of forked dermal bones which connect the pectoral girdle to the epiotic and opisthotic bones of the cranium.
- PTG. Pterygiophore, *os pterygiopherium* (radials, Goodrich, 1930; Berg, 1940). A series of 3 endoskeletal rods which support the dorsal and anal fins. The pterygiophores are composed of 3 segments, a small, rounded distal bone, a short, horizontal middle bone and a long, pointed proximal bone.
- PTO. Pterotic, *os pteroticum* (squamosal, Ridewood, 1904a; pterotic-intertemporal, de Beer, 1937; autopterotic, Harrington, 1955). A pair of mixed (cartilage and dermal) bones which lie on the posterolateral surface of the cranium. They bear the lateral temporal canals.
- Q. Quadrate, *os quadratum*. A pair of triangular endochondral bones which articulate with the angulars of the lower jaw and thus connect the latter with the cranium.
- R. Ribs, *costae*. The paired bones which surround the abdominal cavity and which are attached to the parapophyses or transverse processes. These are the pleural ribs.
- RA. Retroarticular, *os retroarticulare* (angular, Ridewood, 1904a, 1904b; Gregory, 1933; Berg, 1940). A pair of small, triangular endochondral bones which are fused to the posterior corner of the angulars.
- S. Scapula, *os scapulum*. A pair of flat endochondral bones located in the pectoral girdles which articulate anteriorly with the coracoids and posteriorly with the cleithra.
- SC. Sclerotic cartilage, *cartilago sclerotica*. A pair of hemispherical cartilages which surround the eye balls. A small semilunar portion is partially ossified.
- SCL. Supracleithrum, *os supracleithrum*. A pair of curved dermal bones located in the pectoral girdle which connect the cleithra with the posttemporals.
- SE. Supraethmoid, *os supraethmoideum* (dermethmoid, Gregory, 1933; mesethmoid, Goodrich, 1930; Berg, 1940; Chapman, 1941a, 1940b; proethmoid, Dineen and Stokely, 1954; ethmoid, Harrington, 1955). The median dermal ossification that covers the hypethmoid (when present) and the underlying ethmoid cartilage.
- SM. Supramaxilla, *os supramaxillare* (surmaxilla, Ridewood, 1904a; jugal, de Beer, 1937; Vladykov, 1954). A pair of thin, splint-like dermal bones which lie along the dorsal margin of the maxillae.
- SO. Supraorbital, *os supraorbitalium* (circumorbitals, Ridewood, 1904a, 1904b; praeorbital, Vladykov, 1954). Two pairs of small curved bones which form the anterodorsal rim of the orbits. They do not bear sensory canals.
- SOC. Supraoccipital, *os supraoccipitale*. A median bone which covers the posterodorsal surface of the cranium. A prominent crest of bone which extends backward from the endochondral portion is of dermal origin.

- SOP. Subopercle, *os suboperculum*. A pair of thin, flat intramembranous bones which lie below the opercles and overlap the branchiostegal rays.
- SP. Suprapreopercle, *os suprapreoperculum* (supratemporal, Parker, 1873; subtemporal, Gregory, 1933; de Beer, 1937; supraopercle, Holmgren and Stensiö, 1936). A pair of small, tubular intramembranous bones which are present in the salmonines. They lie above the preopercles and transmit the preopercular canal to the pterotic.
- SPO. Sphenotic, *os sphenoticum* (autosphenotic, Holmgren and Stensiö, 1936; Harrington, 1955). A pair of conical endochondral bones which project anterodorsally from the otic region of the chondrocranium. In salmonids the sphenotic is separate from the dermosphenotic.
- SY. Symplectic, *os symplecticum*. A pair of small, pointed endochondral bones which form part of the jaw suspension in bony fishes. They act as braces between the quadrates and the hyomandibulars.
- U. Urohyal, *os urohyale*. A median intramembranous bone which lies in the muscles below the tongue.
- UN. Uroneural, *os uroneurale*. Three pairs of bony plates which lie over the last 3 upturned vertebrae and the urostyle. They are believed to be remnants of neural arches. The larger, more anterior pair is sometimes called the caudal bony plate (Vladykov, 1954).
- US. Urostyle, *cartilago urostyle*. In the restricted sense, this includes only the cartilaginous termination of the vertebral column which in salmonid fishes curves dorsad behind the last 3 upturned vertebrae.
- V. Vomer, *os vomere*. A median dermal bone that is usually toothed and which lies at the anterior extremity of the roof of the mouth.
- VE. Vertebra, *vertebra*. A series of bones which run the length of the body behind the cranium and comprise the vertebral column.

OSTEOLOGY OF THE GRAYLING, *THYMALLUS ARCTICUS*

THE OLFATORY REGION

The olfactory or ethmoid region of the chondrocranium is pyramidal in shape with its anterior or rostral end short and bluntly rounded. Laterally the rostrum bears a cartilaginous knob which articulates with the maxilla anteriorly and with the palatine posteriorly. The slight expansion in this region also forms the anterior boundary of the olfactory capsule. The rounded anterior tip is capped by the paired premaxillae and roofed by the supraethmoid. Posteriorly the cartilage flares into two wing-like ossified projections, the prefrontals (or lateral ethmoids), which constitute the only ossification in the ethmoid complex in the grayling (Plate 1). The prefrontal is mainly endochondral, although there is a lamina of dermal bone on the outer surface. The anterior face of the prefrontal forms the rear margin of the olfactory capsule and its posterior face forms part of the anterior surface of the orbit. Below the prefrontal, a slight cartilaginous prominence provides a posterior articulation for the palatine. This second ethmopalatine articulation has been described by Swinnerton (1902) in *Gasterosteus aculeatus* and by de Beer (1927) in *Salmo trutta* (= *fario*). The cartilage mesial to the prefrontal is perforated by a foramen through which the olfactory nerve and the orbitonasal artery reach the olfactory capsule from the orbit. This is the *foramen olfactorium advehens* of de Beer (1927, 1937) and Böker (1913).

There are two other perforations in the ethmoid cartilage lying mesad of and somewhat above and below the olfactory foramen. These mark the exit of the superior and inferior oblique eye muscles. They meet the pair from the opposite side in the midline, where a deep anterior myodome has been formed in the ethmoid cartilage.

THE ORBITAL REGION

In the grayling little remains of the orbital region of the chondrocranium, it having been preempted by the large eye. The orbitosphenoid is completely lacking, leaving the paired pterosphenoids and the median basisphenoid as the only remaining ossification (Pl. 2, A and C). The use of the term pterosphenoid follows Goodrich (1930: 284), indicating that this bone in teleosts is not homologous with the pleurosphenoid of reptiles or the alisphenoid of mammals. Dorsally a flattened bridge of cartilage, covered by the frontals, connects the ethmoid region with the pterosphenoids. Even less remains of the ventral interorbital septum connecting the prefrontals with the basisphenoid. A median membranous septum separates the orbits. The pterosphenoids are rounded endochondral bones on the posterodorsal face of the orbits. Dorsally they border the large dorsal fontanelles. Posteriorly the pterosphenoids are united by cartilaginous sutures to the sphenotic and prootic bones. Ventrally and mesially the pterosphenoids protect the anterior part of the brain (Pl. 2, A and C). A small foramen for the trochlear nerve lies near the centre of each pterosphenoid.

The median Y-shaped basisphenoid lies just below the ventral part of the pterosphenoid (Pl. 2, A and C). Its short oblique arms articulate with the anterior edge of the prootics slightly anterior of the pituitary body and form the floor of the cranial cavity. The median ventral leg is separated from the parasphenoid by a small extension of cartilage, thus bisecting the posterior myodome. In *Salmo trutta*, according to de Beer (1937: 130), the basisphenoid is phylogenetically a cartilage bone which develops ontogenetically solely in membrane.

The eyeballs are surrounded by hemispherical sclerotic cartilages which have small semilunar ossifications at their anterior and posterior external surfaces. Each of these ossifications constitutes about one-sixth of the corneal perimeter.

THE OTIC REGION

The Otic region is the best ossified part of the chondrocranium. Nearly all bones meet in jagged sutures, interspaced with cartilage, and with little overlap. All except the opisthotics and parts of the pterotics and supraoccipital, are endochondral bones. The most anterior are the subconical sphenotics which border the cartilage around the fontanelles dorsally and the orbit laterally (Pl. 1). They are covered by the frontals and dermosphenotics. The sphenotic is bordered anteromesially by the pterosphenoid, ventrally by the prootic, and posteriorly by the pterotic. Ventrally the sphenotic bears a lateral

fossa for the anterior articulation of the hyomandibular. Its inner surface is hollowed out to receive part of the anterior semicircular canal.

PTEROTIC. The pterotic is of dual origin, dermal and cartilaginous, the components being inseparably fused in the grayling (Pl. 1, A and 2, A). Its outer portion, bearing the lateral temporal canal, is described with the roofing bones. The deeper endochondral part of the pterotic fans out dorsally and ventrally, covering part of the otic capsule. The pterotic meets the sphenotic, dorsally, and the prootic and exoccipital, ventrally. There is a ventrolateral fossa for the posterior articulation of the hyomandibular. Dorsally the dermal part articulates with the frontal and occasionally with the parietal around the rim of the lateral temporal fossa. Its endochondral portion is separated from the dorsal fontanelle and supraoccipital by an expanse of cartilage. Posteriorly the pterotic meets the epiotic and exoccipital bones. This tripartite junction is capped by the small conical opisthotic. The inner surface of the pterotic is irregular and bears a deep cavern for the lateral semicircular canal (Pl. 2, C).

EPIOTIC. The epiotic is a pyramidal-shaped bone forming part of the dorsal and rear surface of the chondrocranium (Pl. 1, A and 2, B). The rounded upper surface of the epiotic lies between the pterotic and the supraoccipital, and forms the intermediate pair of five projections on the rear margin of the chondrocranium. The other projections are lateral wings of the pterotics and the median supraoccipital crest. The posteriorly projecting point of the epiotic serves for the attachment of a strong ligament from the inner surface of the more dorsally directed prong of the posttemporal. Ventrally the epiotic curves inward to meet the exoccipital.

OPISTHOTIC. The opisthotic appears like a small cap over the cartilaginous junction of the pterotic, epiotic, and supraoccipital (Pl. 2, B). It is an intermembranous ossification in the strong ligament from the inwardly directed spine-like projection of the posttemporal, and is the only wholly non-endochondral bone of the otic region. It is so loosely attached to the chondrocranium and is so much a part of the ligament that it often comes off with the posttemporal when the latter is removed.

SUPRAOCCIPITAL. The supraoccipital is a median composite bone covering the caudodorsal surface of the cranial cavity. It is rounded, rising to a crest at the midline (Pl. 1, A and 2, A and B). Here a knob of bone protrudes between the parietals. This knob and the supraoccipital spine are of dermal origin. The supraoccipital extends forward beneath the parietals and forms the posterior margin of the dorsal fontanelles (Pl. 1, A). The dorsal fontanelles are separated by a narrow strip of cartilage (*taenia tecti medialis* of de Beer, 1937) (Pl. 1, A) derived from a posterior extension of the *tectum cranii* similar to that illustrated by Sanderson (1935) in the early development of *Salmo salar*. Less than a third of this median cartilage is ossified by the anterior growth of the supraoccipital, which occasionally extends forward to lie beneath the posterior margin of the frontals. Laterally the supraoccipital is in contact with the epiotics on either

side, but it is denied contact with the exoccipitals or the foramen magnum by a rather large expanse of cartilage. The spine extends caudally and forms a surface of attachment for fascia from the great lateral and protractor dorsalis muscles.

PROOTIC. Ventrally the brain is surrounded by the prootic, which forms the anterior floor of the cranial cavity (Pl. 1, B). It is the largest bone of the chondrocranium and consists of three diverging bony wings. A large expanse of bone extends dorsally to form the anterolateral wall of the brain cavity, another flange extends ventrally partly to enclose the posterior myodome, and a third extends to the midline to form the roof of the posterior myodome. Anteriorly and dorsally the prootic borders the pterosphenoid, sphenotic and pterotic. Posteriorly it is in contact with the exoccipital and basioccipital. Anteriorly and ventrally the prootic meets its mate from the opposite side and the lateral projection of the basisphenoid. The ventrally directed flange of the prootic is overlapped in part by a dorsal outgrowth from the parasphenoid. These two bones, plus the basioccipital, thus form the roof, sides and floor of the posterior myodome. Mesially parts of the anterior and lateral semicircular canals rest on the prootic and form the roof of the sacculus (Pl. 2, C). A vertical strut of bone partially divides the prootic into a portion facing anteriorly and another facing laterally. Three foramina pierce the lateral portion: a blood vessel (the head vein from the orbital sinus, according to de Beer, 1937, for *Salmo trutta*, the jugular canal of Holmgren and Stensiö, 1936) passes through the most ventral and mesial opening, next above is the large, posterior trigeminofacial foramen, and anteriorly is the palatine foramen for the palatine branch of the seventh cranial nerve. In the anterior-facing portion of the prootic the largest and most lateral foramen is the anterior trigeminofacial foramen, the smaller palatine foramen lies dorsal to it, and mesially is found the foramen for the abducens nerve.

BASIOCCIPITAL. The basioccipital forms the posterior floor of the cranial cavity (Pl. 1, B). It is a wing-shaped bone, its anterior flanges are overlapped by the parasphenoid ventrally and are in contact with the prootics anteriorly and with the exoccipitals dorsally. Posteriorly, the basioccipital is circular and articulates with the centrum of the first vertebra (Pl. 2, B). Mesially, it forms the lower halves of the large paired chambers that enclose the sacculus and the sagitta.

EXOCCIPITAL. The large exoccipitals are strongly convoluted and form the greater part of the rear of the cranium (Pl. 2, B). They are prevented from completely surrounding the foramen magnum by a narrow strip of cartilage dorsally and do not quite meet across the basioccipital. Ventrally they almost meet in a pair of rounded articular surfaces, the occipital condyles, which articulate with the atlas. The dorsal wing of the exoccipital meets the epiotic and the pterotic, and is slightly overlapped by the small opisthotic. The anterior wing of the exoccipital meets the prootic in front and borders the basioccipital throughout its ventral edge. The sidewalls of the exoccipital are pierced by the

small glossopharyngeal foramen, anteriorly, and by the larger jugular foramen for the vagus nerve, posteriorly.

OTOLITHS. Three otoliths lie within the auditory capsule. By far the largest is the sagitta, lying within the sacculus (Pl. 16, J3). It has a pointed rostrum anteriorly, and a mesal groove, the sulcus, dividing the otolith into dorsal and ventral portions (Frost, 1925). The asteriscus consists of a microscopic granule lying in the lagena (Pl. 16, J2). The lapillus is slightly larger, but still much smaller than the sagitta; it lies in the utriculus (Pl. 16, J1).

Investing Bones

DORSAL ROOFING BONES

SUPRAETHMOID. The supraethmoid is a small wing-shaped bone lying on the median dorsal surface of the chondrocranium, between the premaxilla and the frontals (Pl. 9, A). It arises as a small median ossification far forward between the premaxillae and grows both laterally and posteriorly. Anteriorly the supraethmoid is expanded to make contact with the ascending processes of the premaxillae, and posteriorly it is deeply bifurcate (Pl. 4), the two prongs thus formed having a number of slender projections which are overlapped by similar serrations from the frontals.

NASAL. The paired nasals are merely bony tubes enclosing the anterior parts of the supraorbital canals (Pl. 4). The cephalic canals of the lateral line system appear to influence the early deposition of bone cells, in that in those bones which bear canals the first ossification appears around the canals and then gradually spreads from these centres. This is true of the frontal, orbitals, extrascapulars and preopercle as well as the nasal. Thus, the nasal is already distinguishable in fish 35 mm in total length. It does not form a sutural connection with any bone but lies in the skin beside the supraethmoid-frontal suture.

FRONTAL. The frontals are large, triangular bones that cover most of the dorsal surface of the chondrocranium, including the dorsal fontanelles, and overhang the orbit laterally (Pl. 9, A). The frontal first makes its appearance in fish of 30 to 40 mm in length as an ossification around the supraorbital canal. Ossification continues in all directions with the greatest expanse of bone located medially and posteriorly from the original centre. The jagged anterior end of the frontal meets the supraethmoid, nasal, prefrontal, and first supraorbital, in that order, from the midline to the side. Laterally, behind supraorbital 1 the frontal forms about 20% of the perimeter of the orbit. At the rear of the orbit, the frontal articulates with the dermosphenotic. Caudolaterally a posterior projection of the frontal meets the dermal crest of the pterotic. The rear margin of the frontal sometimes comes in contact with the lateral temporal fossa, or it may be excluded by extensions of the pterotic and parietal. When in contact with the lateral temporal fossa, the frontal provides for part of the attachment of the lateralis profundus muscle (Greene and Greene, 1913). The remainder of the posterior margin of the frontal forms a broad transverse area of contact

with the parietal and overlaps it slightly. Dorsally, the pair of frontals forms a long and rather irregular suture at the midline, but diverge anteriorly where they are separated by cartilage. From the posterior end of the nasal bone the ossified supraorbital canal extends backward near the middle of the frontal, to a point above the posterior margin of the orbit, where it bends laterally and unites with the infraorbital canal on the dermosphenotic (Pl. 4).

PARIETAL. The paired parietals are irregular in shape and overlies much of the supraoccipital and a small posterior part of the dorsal fontanelles (Pl. 9, A). Each parietal begins as a small dermal centre of ossification some distance laterally of the midline. Each bone is slightly overlapped anteriorly by a backward growth of the frontal, and laterally it forms most of the dorsal border of the lateral temporal fossa. Posteriorly the parietals cover not only the supraoccipital but also part of the epotics, and are themselves hidden by the extrascapulars. The parietals meet at the midline, except posteriorly, where they are separated by a small projection of the supraoccipital (Pl. 4).

EXTRASCAPULAR. The extrascapular bones consist of 2 or 3 bones on each side and a single median one in a transverse series over the posterior region of the skull between the parietals and the posttemporals (Pl. 9, A). They arise as separate centres of ossification surrounding the supratemporal canal. All are moderately expanded throughout (Pl. 4). The most lateral extrascapular is in contact with the ventral expansion of the posttemporal. The others continue in a half circle over the roof of the skull, to the posttemporal of the opposite side. They overlies and partly hide the pterotics, epiotics, supraoccipital, and parietals. Passing backward through the pterotic, the lateral canal enters the lateral extrascapular, where it is joined by the supratemporal canal, and transmits the combined branch backward to the posttemporal bone.

Only the posteriorly directed crest of the supraoccipital is seen from dorsal aspect (Pl. 9, A). The remaining endochondral portion is part of the otic capsule. The supraoccipital crest projects beyond the median extrascapular and between the dorsally directed prongs of the posttemporals. The crest forms a broad area of attachment for the protractor dorsalis muscle of the trunk (Greene and Greene, 1913).

The paired posttemporal and the pterotic bones are seen in part from dorsal view. The posttemporals are discussed with the pectoral girdle. The ectosteal portion of the pterotic (supratemporal-intertemporal, Holmgren and Stensiö, 1936; intertemporal, de Beer, 1937; membranopterotic, Harrington, 1955) originates as a small tubular bone enclosing the lateral temporal canal. Shortly after ossification commences the dermal part becomes fused with the underlying cartilaginous component. Anteriorly the pterotic articulates with the frontal and the dermosphenotic and receives the lateral canal from the dermosphenotic. Dorsally the pterotic forms the ventral margin of the lateral temporal fossa, and posteriorly it comes very near but usually does not touch the lateral extrascapular or the opercle. Ventrally and mesally the dermal portion of the pterotic curves inward and fuses with its cartilaginous component just dorsal of the articula-

tion with the hyomandibular. About midway in the pterotic, the lateral temporal canal is joined by the preopercular canal. Between the preopercle and the pterotic, the preopercular canal is membranous in the grayling; the tubular bone or suprapreopercle of the Salmoninae is absent (P. 10, B and C).

LATERAL SKULL BONES

Viewed from lateral aspect the head of *Thymallus arcticus* is almost completely invested in bone, except for the large orbit, the part of the adductor mandibularis muscle seen below the postorbitals, and the small part of the opercular muscles just above the dorsal tip of the preopercle.

PREMAXILLA. The premaxillae are a pair of slightly curved, somewhat triangular bones which comprise the anterior end of the upper jaw and the border of the anterior third of the gape (Pl. 10, B). They meet in a loose median suture in the adult. Each bone bears an anterior flange, to which a single series of 8 to 12 sharp conical teeth are attached, and a posterodorsal process which articulates with the anterolateral margin of the supraethmoid (Pl. 4). The remainder of the bone forms the anterior margin of the olfactory capsule. The lateral portion of the premaxilla overlaps the narrow mesal prong of the maxilla to which it attaches by a ligament and by which it is separated from the palatine. The mesal portion of the premaxilla curves around the anterior extremity of the rostral cartilage, which separates it from the vomer ventrally. Each premaxilla arises as a small intramembranous ossification at the anterior tip of the ethmoid cartilage, and the teeth arise separately but grow toward the bone and fuse with it.

MAXILLA. The maxilla, a thin bone comprising about two-thirds of the upper border of the gape, arises as a thin, splint-like ossification. The curved anterior end of the maxilla slips behind the premaxilla, where on one side it articulates with the premaxilla and on the other it articulates with the palatine. These are its only points of articulation. It is attached by skin and ligaments, dorsally and laterally, to the lachrymal, suborbitals, bones of the palate, and bones of the lower jaw. It bears a single file of 15 to 22 teeth except at the anterior and posterior ends of the bones, which are toothless (Pl. 4). The teeth arise separately, grow toward the maxilla, and fuse with it.

SUPRAMAXILLA. The single pair of supramaxillae lie on and partly cover the dorsal margin of the posterior half of the maxillae (Pl. 10, B). The supramaxilla is thin, narrow, and tapered at both ends, and like the maxilla it has cutaneous attachments to the suborbitals and bones of the palate (Pl. 4). It makes a belated appearance, long after the maxilla and teeth are fairly well ossified.

CIRCUMORBITAL SERIES. Ridewood (1904a; 69) has pointed out that because of the variation exhibited by the circumorbital bones no great morphological importance can be expected from a comparative study of them. This is true of the postorbitals of *Thymallus arcticus*, although the supraorbitals and the lachrymal remain constant in number and general shape. The circumorbital

series consists of 8 (occasionally 7) bones surrounding the greater part of the orbit, except for the part bordered by the frontal (Pl. 10, B). Authors have applied different names to the bones of the orbital series, for example Ridewood (1904b), Berg (1940) and Vladykov (1954). In the present treatise, the two anterodorsal bones are the supraorbitals, the anteroventral element is the lachrymal, the ventral bone is the infraorbital, the remaining posterior bones are postorbitals, of which the uppermost is the dermosphenotic. The supraorbitals are the only bones of the series which do not bear a sensory canal, and the area in which these bones develop is the last to ossify.

Supraorbital number 1 is small and somewhat arched dorsally (Pl. 4). Continuing from the rim of the frontal, it forms the anterodorsal margin of the orbit. Anteriorly it lies over the prefrontal, which it may touch without articulation. Its anteriormost tip forms a narrow contact with supraorbital 2.

Supraorbital number 2 is unlike the other circumorbital bones (Pl. 4). It is narrow and U-shaped, forming part of the anterior margin of the orbit and the posterior margin of the nasal capsule. One of its arms curves inward to overlap the prefrontal. Ventrally it forms a broad suture with the lachrymal.

The lachrymal is roughly rectangular in shape with a small dorsally directed projection (Pl. 4). It forms part of the anterior rim of the orbit and lies just above the maxilla. It carries the anterior extension of the infraorbital canal, where that canal branches into 3 to 5 short canals that terminate in external pores. The lachrymal articulates anteriorly with supraorbital number 2, and posteriorly with the infraorbital.

The infraorbital bone is thin and subtriangular, with the apex pointing forward (usually more attenuate than in the specimen figured, Pl. 4). The apex projects beneath the lachrymal for a short distance. It carries the infraorbital canal; it articulates with the lachrymal anteriorly, and with postorbital number 1 posteriorly.

Postorbitals 1, 2, and 3 are thin plates forming the posterior rim of the orbit. They are similar in shape, although postorbital 1 narrows anteriorly where it meets the infraorbital (Pl. 4). These bones almost completely cover the large adductor mandibularis muscle and touch the preopercle along part of their posterior margins (Pl. 10, B). These are the most variable of the circumorbitals, occasionally fusing to form two bones instead of 3. All carry the infraorbital canal. Dorsally postorbital 3 articulates with the dermosphenotic. This bone differs little from the other postorbitals but it is distinctive in being somewhat smaller and in bearing the junction of the supraorbital and infraorbital canals to form the lateral canal (Pl. 4). The dermosphenotic articulates dorsally, with the frontal, and ventrally with postorbital 3. It borders the orbit anteriorly, and the pterotic posteriorly (Pl. 10, B).

DENTARY. The dentaries are a pair of V-shaped bones forming the major supports of the lower jaw (Pl. 4). Their apices meet anteriorly in a loose symphysis and their two limbs curve sharply around the margin of the jaw. The upper limb is shorter, and its anterior three-fourths bears a single row of approxi-

mately 18 teeth. It connects posteriorly to the rear end of the maxilla by a fold of skin and draws that bone into a vertical position as the lower jaw is depressed, thus widening the gape. The lower limb is longer and encloses the mandibular canal. This limb extends caudad as far as the quadrate but does not touch the retroarticular (Pl. 4). The crotch of the dentary envelops the angular, and Meckel's cartilage is almost completely embedded in nearly the entire length of its mesal surface (Pl. 5). The anterior part of the dentary is endochondral, and is termed the mentomeckelian bone (de Beer, 1937; Harrington, 1955). It is continuous with the intramembranous part of the dentary, which commences early as two ridges corresponding to the two limbs.

ANGULAR. The angular is the second largest bone in the lower jaw (Pl. 4); only the dentary is larger. The angular is a controversial bone, because its origin and development are somewhat obscure (de Beer, 1927, 1937; Haines, 1937; Harrington, 1955). Most past writers have termed it the articular, but the findings of Haines (1937) and Lekander (1949), discussed by Berg (1940: 416) and Harrington (1955: 284), demonstrate the desirability of applying the name angular. The small bone at the ventrocaudal end of the mandible, commonly termed angular in the past, may be called the retroarticular (Harrington, 1955: 287). The bone here termed the angular arises, in part, as an endochondral ossification at the posterior end of Meckel's cartilage, but most of it arises intramembranously. The angular is thin and toothless. It forms an acute angle anteriorly where it slips into the dentary, and it is arched in cross section throughout most of its length, the grooves on its mesal surface being occupied by Meckel's cartilage. Lying well back on the cartilage is the coronomeckelian (Pl. 5). The angular is massive posteriorly; on its upper surface there is a deep transverse depression, which articulates with a ventral bar on the quadrate. The mandibular canal passing from the preopercle to the dentary penetrates the outer face of the angular with a short, oblique tube (Pl. 4). As usual, ossification appears early around this sensory canal. Like the dentary, the upper margin of the angular is connected to the maxilla by a fold of skin. A ligament attaches the posterior end of the angular to the preopercle.

RETROARTICULAR. The retroarticular is a small triangular bone located at the caudoventral corner of the mandible (Pl. 4 and 5). It is inseparably fused to the angular, and in the grayling does not come in contact with the articular facet. It is composed mainly of dermal bone although it does have a small core of endochondral material.

CORONOMECKELIAN. The coronomeckelian (Harrington, 1955: 285), usually called sesamoid articular, is a small triangular bone of dermal origin, located on the mesal surface of the angular bone and loosely attached to Meckel's cartilage (Pl. 5). It provides for a part of the insertion of the adductor mandibularis muscle, and according to Ridewood (1904a) is an ossified tendon.

PREOPERCLE. The preopercle, despite its name, does not belong to the opercular series (Ridewood, 1904a; Hubbs, 1919). The preopercle carries the

sensory canal of the same name and is therefore likened to the circumorbitals by some workers (Ridewood, 1904a; Westoll, 1937). Functionally the preopercle serves in several ways: its anterior margin offers a broad area for the origin of the large adductor mandibularis muscle, its expanded posterior part helps shield the gills, and it carries the preopercular canal. It arises as a narrow arched ossification in close proximity to the canal, and expands posteriorly and ventrally with growth. It is sculptured with branches of the sensory canal, especially in its expanded ventral part, where occasionally 3, but usually 4 pores open to the exterior. The preopercle of the adult grayling is prominently arched; the horizontal arm is about two-thirds the length of the vertical arm (Pl. 4). The preopercle does not articulate with any other bone, but the anterior tip of its horizontal arm is attached to the jaw articulation by a strong ligament. Mesally the preopercle covers part of the ceratohyal, epihyal, quadrate, symplectic, hyomandibular, the three opercular bones, and all of the interhyal, to which it is attached by skin and ligaments. Anteriorly the postorbitals usually touch the preopercle along the length of the vertical arm (Pl. 10, B). Dorsally the preopercular canal is transmitted directly to the pterotic, as the grayling does not have a suprapreopercular bone.

OPERCULAR SERIES. The larger elements of the operculum are believed to be expanded branchiostegal rays, homologous with the saber-like rays. All elements of the opercular series are entirely dermal in origin. The opercle is the largest bone in the grayling skull. It is thin, smooth and rectangular and covers much of the gill arches (Pl. 4). It first appears as a small dermal ossification around the articulation with the hyomandibular, and spreads backward and downward from this point. The anterior border of the opercle is overlapped by the preopercle (Pl. 10, B) and ventrally it narrowly overlaps the subopercle. The latter denies the opercle contact with the interopercle. Dorsally it is free, but here it partially covers the dilator operculi, levator operculi, and adductor operculi muscles, all of which insert on the mesal surface of its dorsal half (Greene and Greene, 1913). When the opercle is closed, the posterior border of the opercle extends over the anterior part of the supracleithrum. The inner surface of its anterodorsal corner is thickened and has an oval depression for articulation with the hyomandibular.

The subopercle, when it first ossifies, looks very much like a thin, flat, branchiostegal ray, but later it expands posteriorly into a flat plate (Pl. 4). Its ventral border overlaps the last (9th or 10th) branchiostegal ray; anteriorly, it is partly covered by the interopercle, and its small pointed, proximal projection is hidden by the preopercle (Pl. 10, B). When the operculum is closed, the dorsal edge of the subopercle covers the anterior part of the cleithrum, supracleithrum, and first postcleithrum.

The interopercle is a thin triangular bone covering the lower part of the gill region (Pl. 4). It originates as a small triangular ossification much like the branchiostegal rays, except that it is out of position and does not form a series with them. For this reason, some workers (e.g. Ridewood, 1904a) consider it to belong with the preopercle rather than in the branchiostegal series. Hubbs

(1919), however, included it with the latter group. Ventrally the interopercle partly covers the last branchiostegal ray and the epihyal bone; posteriorly it overlaps the subopercle (Pl. 10, B); while anteriorly and dorsally nearly half the bone is hidden by the preopercle.

The branchiostegal rays first appear as thin bony strips on the ventrolateral side of the head. The usual number is 9 or 10, and there may be 9 on one side and 10 on the other. The first anteroventral ray is the smallest, and those above are progressively longer and more expanded (Pl. 10, B). The first 6 or 7 rays are attached to the ceratohyal and the upper 3 to the epihyal bone. They are arranged in a series with each ray partly overlapping the one in front of it.

VENTRAL BONES OF CRANIUM

VOMER. The vomer, is a small, oval, median bone in the anterior part of the roof of the mouth (Pl. 4). Ventrally it carries 7 or 8 weak teeth which are borne on two ridges which project from the rest of the bone. Dorsally the vomer is convex upward in transverse and longitudinal sections (boat-shaped), the dome fitting into a depression in the cartilaginous rostrum. Anteriorly the vomer is curved to conform to the border of the rostrum and posteriorly it consists of two acute prongs which overlap the parasphenoid. The vomer arises intramembranously as a small rounded ossification.

PARASPHENOID. The parasphenoid is a long, narrow intramembranous bone covering most of the ventral surface of the chondrocranium (Pl. 4). It bears a marked dorsal ridge, which fits into a groove in the cartilaginous ethmoid and interorbital septum, from near the anterior tip to as far back as the basisphenoid. In the midline is a small, spine-like dorsal projection that points towards the basisphenoid and is joined to the ventral leg of that bone by cartilage. Behind this projection, the parasphenoid forms a deep trough, having lateral flanges of bone that curve dorsad to form the floor and part of the side walls of the posterior myodome. These flanges contact similar downward-projecting flanges from the sides of the basioccipital and both prootics. Anteriorly the flanges are somewhat elevated and serrate; behind this they are smooth and straight (Pl. 4). The V-shaped posterior end of the parasphenoid does not quite touch the atlas, but it does leave a posterior opening in the myodome. Anterolaterad of the median dorsal spine are a pair of foramina through which the internal carotid arteries pass. Posterolaterad of the same spine, the posterior palatine branch of the facial nerves pass through a second pair of foramina. In lateral aspect, the parasphenoid is bent abruptly downward at the level of the palatine foramina, the bone rising gradually both before and behind that point.

Visceral Arches

INTRODUCTION

The bones discussed in this section are homologous to the cartilaginous elements of the upper jaw, hyoid arch and the 5 branchial arches of the shark. The bones of the palatoquadrate no longer border the gape, but constitute an

"inner jaw", primarily concerned with jaw articulation and development of the palate. The remainder of the primitive mandibular segment (Meckel's cartilage) was discussed with the bones of the lower jaw, namely the dentary and the angular. The hyoid apparatus suspends the jaws from the cranium and, through the hypohyals, provides the anterior and inferior skeletal support of the gill arches. The first 4 branchial arches support the gills. The 5th arch is incomplete and does not function in respiration.

PALATOQUADRATE ARCH

PALATINE. The palatine is a splint-shaped bone of mixed origin. It arises as a thin strip of cartilage running forward from the quadrate and lying beneath the orbit (autopalatine of Allis, 1897: 772). Ventrad of the endochondral part there appears a separate dermal ossification, the dermopalatine (Allis, 1897: 772). Below the dermopalatine, the teeth appear as individual centres of ossification. The teeth fuse to the lower edge of the dermopalatine and the latter fuses with the autopalatine to form the mixed palatine bone. The anterior end of the palatine is larger and bears 8 to 12 small, somewhat retrorse teeth that form a single irregular row (Pl. 5). The palatine articulates mesally with the chondrocranium at two points, one in front and one behind the nasal capsule, in a manner described by Swinnerton (1902) for *Gasterosteus aculeatus*, by de Beer (1927) for *Salmo trutta*, and by Saunderson (1935) for *Salmo salar*. The anterior or rostro-palatine articulation (de Beer, 1937) bears a cartilaginous knob which fits into a depression formed partly by the incurved maxilla and partly by the enlargement of the rostrum. The posterior ethmopalatine articulation (de Beer, 1937) consists of a small cartilaginous projection which attaches to the ethmoid cartilage just beneath the prefrontal. The remainder of the lateral edge of the palatine is separated from the mesopterygoid by a strip of cartilage. The posterior end of the palatine is slightly overlapped by the ectopterygoid, thus separating the former from the quadrate. The lateral margin of the palatine has a ligamentous attachment to the maxilla.

ECTOPTYERGID. The ectopterygoid is a small, curved, dermal ossification forming the lateral margin of the palate (Pl. 5). Its dorsal border lies near the mesopterygoid but is narrowly separated from it by cartilage. Posteriorly the ectopterygoid lies against the anterior border of the quadrate, and anteriorly it is in contact with the palatine. The ventral margin of the ectopterygoid is free, being connected to the maxilla by a loose fold of skin.

QUADRATE. The quadrate is a fan-shaped endochondral bone articulating with the depression in the angular (Pl. 5). The area on and around its articular condyle is the first to ossify during development. Dorsally the quadrate is separated from both the mesopterygoid and metapterygoid by a narrow strip of cartilage, the palatoquadrate cartilage, which continues forward and meets the palatine. Posteriorly the quadrate bears a thin, acuminate strut of dermal bone, the grooved lower side of which receives the upper edge of the horizontal limb of

the preopercle. Between this strut and the main part of the quadrate lies the symplectic, connecting the quadrate with the hyomandibular.

MESOPTERYGOID. The mesopterygoid lies just in front of the metapterygoid. It is a thin triangular bone whose dorsal edge is directed inward, with most of the expanded surface lying under the eyeball (Pl. 5). It covers much of the palate but does not quite touch the parasphenoid. The hind border is overlapped by the metapterygoid and is separated from the quadrate by a bridge of cartilage. The entire outer margin of the mesopterygoid is bordered by the ectopterygoid and the palatine, and the pointed anterior end touches the ethmoid cartilage beneath the prefrontal. It arises intramembranously, ossification beginning at its outer margin.

METAPTERYGOID. The metapterygoid is a semilunar endochondral bone fitting into the curve formed by the quadrate, symplectic, and hyomandibular. Anteriorly it bends slightly inward, forming a part of the ledge on which the eyeball rests (Pl. 5), and overlapping the posterior margin of the mesopterygoid. Dorsally it is free, forming part of the lateral wall of the pharynx. Posteriorly it overlaps the lower part of the hyomandibular, and ventrally it is connected to the symplectic and quadrate by a narrow strip of cartilage.

HYOID ARCH

HYOMANDIBULAR. The hyomandibular is a hatchet-shaped endochondral bone that suspends the jaws from the cranium (Pl. 5). It contains a hyomandibular foramen, through which a branch of the facial nerve passes. The foramen extends from the mesal surface of the upper part of the bone to the deep groove below the posteriorly directed opercular condyle. Anteriorly on the bone is a thin dermal flange that is overlapped by a posteriorly directed process from the metapterygoid. Dorsally the hyomandibular articulates with the sphenotic and pterotic, by an elongate condyle that retains a cartilaginous surface. Below the opercular condyle, the ventral projection of the hyomandibular is overlapped by the preopercle. Ventrally the hyomandibular is connected to the symplectic and the interhyal by a wedge of cartilage. The hyomandibular is overlain by the large adductor mandibularis muscle and by the postorbitals. Ossification first appears in a Y-shaped cartilaginous area around the hyomandibular foramen.

SYMPLECTIC. The symplectic, an endochondral bone peculiar to fishes, serves as a brace for the articulating bones of the jaw. It is shaped like a marlin spike, pointed anteriorly, where it is in contact with the quadrate (Pl. 5). It is united to the hyomandibular and metapterygoid by a narrow bridge of cartilage.

INTERHYAL. The interhyal is a small, cylindrical endochondral bone which connects the posterodorsal tip of the epihyal with the triangular piece of cartilage which separates the symplectic from the hyomandibular, and thus suspends the lower hyoid elements from the hyomandibular (Pl. 5).

EPIHYAL. The epihyal is a semilunar bone of endochondral origin. Its broad anterior end articulates with the ceratohyal, and the posterodorsal tip is connected to the interhyal (Pl. 5). Three branchiostegal rays are borne on the epihyal.

CERATOHYAL. The ceratohyal is a flat endochondral bone extending along the side of the pharyngeal cavity. Both ends are somewhat expanded, the wider posterior end articulates with the epihyal, and the narrower anterior edge joins the hypohyals (Pl. 5). Six or 7 branchiostegal rays are suspended from it.

HYPOHYAL. The hypohyals consist of two pairs of conical endochondral bones connecting the pair of ceratohyals with the median basihyal. Both the upper (smaller) and lower (larger) hypohyals meet their fellows from the opposite side at the midline, in a suture that is covered dorsally by the first two (median) basibranchials (Pl. 5). The upper and lower hypohyals are separated by cartilage where the anterior cartilaginous tip of the ceratohyal meets the hypohyals. Anteriorly the hypohyals join the basihyal cartilage.

BASIHYAL. The median basihyal forms the base of the tongue (Pl. 5 and 6, C). It is entirely cartilaginous, but it is covered dorsally by a thin, spatulate, dermal ossification, the lingual plate (Pl. 5 and 6, C), which bears a central patch of weak teeth. Posteriorly the basihyal articulates with the paired hypohyals, their junction lying beneath the first basibranchial. The hyoid elements of the grayling are similar to those of *Salmo salar* which have been described by Tchernavin (1938b).

BRANCHIAL ARCHES

The branchial skeleton of the grayling is largely endochondral in origin, and much of the cartilage is retained, especially at the articular surfaces and in the anterior and posterior copula (Tchernavin, 1938b). Only the dentigerous pharyngeal plates are intramembranous.

PHARYNGOBRANCHIALS. There are 3 pairs of Y-shaped pharyngobranchials, each with 3 articular surfaces (Pl. 6, C). Only the first bone in the series is attached to the ventral surface of the parasphenoid. Its remaining two articular surfaces are joined to the epibranchial of the first arch and to a knob of cartilage which connects with the pharyngobranchial of the second arch, respectively. The second pharyngobranchial has a broad lateral base that is in contact with its own epibranchial, and an anterior petiole-like branch that makes contact with the epibranchial of the first arch. A broad projection with an expanded mesal end connects with slender prongs from the 1st and 3rd pharyngobranchials. The third pharyngobranchial articulates broadly with its own epibranchial and by slender branches with the epibranchial and the pharyngobranchial of arch 2. The 3rd pharyngobranchial bears a small toothed plate on its lower surface (Pl. 6, C). A small piece of cartilage, regarded as the pharyngobranchial of the 4th arch, connects epibranchial 4 with the expanded lateral wing of pharyngobranchial 3. The pharyngobranchials are without gill rakers.

EPIBRANCHIALS. The first 4 pairs of branchial arches have epibranchials. The first three of these are similar, each bearing a well-developed posterior prong, mentioned above, and a deep groove on its upper surface which forms a protective cradle for the afferent and efferent branchial arteries. The 4th epibranchial has an expanded dorsal portion and a toothed pharyngeal plate lying partly on its ventral surface and partly on the cartilaginous 4th pharyngobranchial (Pl. 6, C). The plate is not fused to the branchial bones. The first 3 pairs of epibranchials bear short gill rakers both anteriorly and posteriorly, but those on the posterior edge are much smaller and fewer in number. The 4th epibranchial, however, bears no gill rakers.

CERATOBANCHIALS. There are 5 pairs of ceratobranchials (Pl. 6, C). They are the longest bones in the branchial arches. Each one, except the last, has a groove on its ventral surface which partly surrounds the branchial arteries. All 5 ceratobranchials bear gill rakers on their anterior edges, but those on the posterior edges are shorter, and they are lacking altogether on the fifth. The 5th ceratobranchial is somewhat expanded near its base, and it bears a toothed pharyngeal plate on its dorsal surface (2 in one specimen). The first 3 ceratobranchials articulate anteromesially with their hypobranchials and the last two articulate with the posterior copula.

HYPOBRANCHIALS. Only the anterior 3 arches possess hypobranchials. The first two are similar and both articulate with the anterior copula at the cartilaginous bridges between the basibranchial bones. The 3rd hypobranchial is widest at its articulation with the ceratobranchial, becoming narrower as it arches around the 4th basibranchial (Pl. 6, C). All three bear short gill rakers on their anterior edges only.

BASIBRANCHIALS. The 4 basibranchial bones lie in a median series on the floor of the pharynx (P. 6, C). These, together with interspaced cartilage, constitute the anterior copula (Tchernavin, 1938b: 350). The posterior copula, composed of a broad plate and a tail piece lying between the 5th ceratobranchials, is entirely cartilaginous. The 3rd pair of hypobranchials connect the posterior copula with the 4th basibranchial of the anterior copula. The 1st basibranchial lies between the hypohyals; anteriorly it joins the basihyal cartilage and, posteriorly, it forms a suture with the 2nd basibranchial, without intervening cartilage. In the grayling, the basibranchials are not covered by a basibranchial plate.

UROHYAL

UROHYAL. The urohyal does not belong to the branchial skeleton but arises as an intramembranous bone (Ridewood, 1904a: 76); it is included here only for convenience. The small, rounded anterior knob of the urohyal is attached to the hypohyals by a ligament. Posteriorly, the urohyal broadens to form lateral flanges on its ventral surface. The thin crest extends dorsally like a sail, with a jagged posterior margin (Pl. 5). The urohyal is located dorsal of the branchio-

stegal rays, the intermandibularis, geniohyoideus, and hyohyoideus muscles. The urohyal is the ossified tendon of the sternohyoideus muscles, in which it is embedded. The muscles originate at the anterior ends of the cleithra and coracoids and run forward to insert on the hypohyals and the dorsal crest of the urohyal.

Axial Skeleton

VERTEBRAL COLUMN

The vertebral column is composed of 59 to 61 vertebrae (58 to 62 in *T. arcticus baicalensis* and 56 to 61 in *T. thymallus*, Svetovidov, 1936), counting all distinguishable centra but not the largely cartilaginous urostyle, in the manner of Vlad'ykov (1954) and Andrews and Lear (1956). Of these, 36 to 39 are trunk vertebrae and 21 to 23 are caudal vertebrae with haemal spines.

The centra are hour-glass shaped and amphicoelous, and each is perforated by a small median canal. The hollowed out spaces between the centra, as well as the canals are filled with the remains of the notochord. The first vertebra, or atlas, articulates with the basioccipital and with the exoccipitals; it varies in size, but is usually shorter than the other centra. The second vertebra is somewhat larger, and the remaining ones increase in size to the middle of the trunk region, after which they gradually decrease in size. The lateral face of each centrum is marked by horizontal bony ridges which are areas of origin and insertion for fascia from the myotomes.

Dorsally the centra bear neural arches which are larger and heavier cranially, and become smaller and lower caudally (Pl. 7, A and B). The neural arches bear paired anteriorly and posteriorly directed projections, the dorsal pre- and postzygapophyses (Pl. 7, B). The prezygapophyses do not quite touch the postzygapophyses. The neural arches terminate in posteriorly directed neural spines (Pl. 7, A). Those lying before and below the dorsal fin consist of separate lateral elements, most of the remainder are fused above the neural cord to form acute conical spines, and the last 6 or 7 are blunt and flat (Pl. 7, C). The anterior neural arches are broad and occupy the entire length of each centrum, with the spines emerging above the middle of the vertebrae (Pl. 7, A). The first 24 to 26 neural arches are not co-ossified with the centra, a feature characteristic also of the Argentinidae and Clupeidae (Ford, 1937: 36). In the tail region, the neural arches are firmly fused to the centra, are tilted more strongly caudad and the spines emerge farther forward over the centra (Pl. 7, B).

Epineurals, small dorsolateral intermuscular bones, articulate with the bases of the neural arches along the first 25 to 28 vertebrae (Pl. 7, A). All are about the same length, but the more posterior ones articulate higher on the neural arches.

The vertebrae bear paired ventral transverse processes, parapophyses, which occupy most of the length of each centrum. The parapophysis of the atlas consists merely of a bony nodule and does not have a rib. That of the second vertebra is somewhat atypical and occasionally supports a short rib. Approximately the first 25 parapophyses, including the above two, lie in pits in the centra (Pl.

7, A). They are not fused to the centra but are held firmly in place by ligaments (Ford, 1937). The parapophyses bear ventral pre- and postzygapophyses which function as articulating surfaces for the vertebrae (Pl. 7, B). The ventral prezygapophyses in the anterior trunk region are somewhat better developed than the postzygapophyses; each has an anterior projection which extends forward toward the centrum next anterior but does not quite articulate with the postzygapophysis.

Behind these anterior 26 vertebrae, the transverse processes increase in length and are ankylosed to the centra. A transverse bony bridge connects the transverse processes in each of the 2 or 3 most posterior trunk vertebrae, thus forming a closed haemal arch on each vertebra. The remaining haemal arches of the more posterior vertebrae project ventrally, forming haemal spines (the distinguishing feature of the caudal vertebrae, Pl. 7, B). The haemal spines of the posterior 8 to 10 vertebrae are gradually expanded into the hypurals of the tail. The haemal canal contains the caudal artery and vein, and is open as far as and sometimes through the first hypural.

The ventral or pleural ribs curve ventrally between the muscles and peritoneum around the peritoneal cavity, ending in cartilaginous points near the midline. The ribs belonging to vertebrae 3 through 20 are best developed, being larger and longer, and somewhat expanded dorsoventrally. These also have a T-shaped head, with surfaces which articulate with the parapophyses (Pl. 7, A). The more posterior ribs have progressively blunter, flatter heads, which are attached by ligaments near the tips of somewhat lengthened transverse processes. These ribs also decrease in size, caudally, until the last is little more than a bony spur, similar in form to a haemal spine. There are from 35 to 38 pairs of ribs; the first and occasionally the last trunk vertebrae do not bear ribs. From the bases of ribs 3 through 10, short epipleural ribs project caudally (Pl. 7, A) as spine-like intermuscular processes.

The caudal fin of the grayling is a large forked structure consisting of 7 or 8 centra, modified neural and haemal structures, and fin rays. It is finely scaled far out on the rays, especially on the dorsal and ventral lobes. The last 7 or 8 vertebrae are somewhat modified to support the fin, regressing in size and carrying expanded neural and haemal spines which project backward. As in other salmonid fishes, the 3 terminal vertebrae are upturned and become progressively smaller. The antepenultimate vertebra is only slightly upturned and is usually intermediate in size and shape between the two adjacent vertebrae. The last vertebra with a discernible centrum is the most highly modified.

Of the modified neural spines (from the last 8 vertebrae) the anterior 3 or 4 are fused with the neural arch, the next 1 or 2 are free from the neural arch (Pl. 15, C), and the 2 epurals are free from the anterior (first) uroneural (Pl. 7, C). The first uroneural and the 3 neural arches before it are free from the centra. The anterior uroneural has 2 small dorsal depressions which act as articulating surfaces for the epurals. The caudal ends of the epurals are almost straight across, similar to the hypurals.

Three pairs of uroneurals are present, beside and partly covering the last

4 centra and the urostyle (Pl. 7, C). The uroneurals are readily distinguishable since they are paired structures, whereas the epurals are unpaired. Regan (1910) and Hollister (1936) interpreted the uroneurals as specialized neural arches. Both of these authors included among the uroneurals the caudal bony plate of Vladykov (1954) or extra neural arch of Dineen and Stokely (1954). Except for a difference in position, there is no apparent reason to doubt that these 3 pairs of bones are serially homologous. The anterior uroneural is a paired bone covering the dorso-lateral surface of the last 3 or 4 centra; it bears a posterior projection that extends well onto the urostyle (Pl. 7, C). The anterior uroneural is forked, the more lateral limb of the fork being slightly longer. The dorsal crest is small. The second uroneural, lying dorsolateral of the urostyle, is larger than the third and partly covers both the first uroneural and the urostyle. The ventrolateral surface of the small third uroneural overlies the urostyle (Pl. 7, C).

The vertebral column terminates in the cone-shaped urostyle. The urostyle is curved abruptly dorsad beyond the last centrum and terminates near the bases of the longest rudimentary caudal rays (Pl. 7, C). Although usually considered cartilaginous in the Salmonoidei, the urostyle is not completely so in the adult grayling. Two or 3 bony nodules are embedded in a cartilaginous matrix, the largest nodule being an ossified core just beyond the terminal centrum.

Developmentally, ossification commences earlier around the upturned notochord than it does farther forward. In this posterior area, the first uroneural shows signs of ossification simultaneously with the appearance of bony material in the neural arches just in front of it. The penultimate and ultimate centra begin to ossify before the 5 or 6 centra anterior to them. The first uroneural appears to be formed by a fusion of the posterior neural arches belonging to at least the last 3 vertebrae. The 2 epurals are probably modified neural spines which have not become fused to the first uroneural. It is interesting that the 1 or 2 neural spines just anterior of the epurals ossify separately from their neural arches and do not fuse with the latter even in the adult (Pl. 7, C).

Haemal spine modification begins with those belonging to the last 7 or 8 caudal vertebrae (Pl. 7, C). There is a broadening of both the haemal arch and spine, with the distal end becoming flat and expanded. The haemal spines lying ventral of the urostyle and the last 3 centra are the most highly modified and are termed hypurals. They support the principal caudal fin rays. In the grayling, there are 7 hypurals and 5 other modified haemal spines anterior of them (Pl. 7, C). Developmentally ossification commences in the haemal arches and spines a little before bony material is present in the centra. The first (and sometimes the 2nd) modified haemal arch (8th last vertebra) is most often fused to its centrum. The remainder, including the hypurals, are autogenous (Regan, 1910). The 7 hypurals are numbered, starting anteriorly with number 7 lying nearest the urostyle. Hypural 1 is associated with the 1st (antepenultimate) upturned caudal vertebra; hypurals 2 and 3 are associated with the 2nd (penultimate) upturned vertebra; hypurals 4 and 5, with the terminal (ultimate)

vertebra; and hypurals 6 and 7, with the urostyle (Pl. 7, C). Since the hypurals are modified haemal spines this distribution suggests that each of the last 2 vertebrae and the urostyle represents 2 fused centra, 6 in all.

The caudal fin rays are supported by the modified neural spines, epurals, urostyle, hypurals, and modified haemal spines. The long rays which extend the whole length of the fin are counted separately from the short rudimentary rays that are located dorsally (epaxial) and ventrally (hypaxial). All principal rays are branched, in the adult, except the outer dorsal and ventral rays. The frequencies of occurrence of the principal rays of 15 *T. arcticus* were as follows: 17 (1), 18 (3), 19 (11); whereas 11 specimens of *T. thymallus* yielded the following counts: 18 (4), 19 (7).

MEDIAN FINS

Thymallus arcticus is characterized by its long dorsal fin, with between 18 and 25 rays including the short, crowded forward rays. Counts made on 11 specimens of *T. thymallus* yielded the following distribution: 18 (1), 19 (6), 20 (4), whereas Svetovidov (1936: 215) reported 17 to 22 rays in *T. arcticus baicalensis*. The first 8 or 10 rays are unbranched but all are paired. Each ray is supported by a chain of 3 pterygiophores. These include a small rounded pterygiophore which is clasped between the base of each paired ray. The 2nd series of pterygiophores are somewhat larger, rod-like and function as spacer bars between the bases of the rays. The 3rd series are long, dorsally expanded pterygiophores which insert between the neural spines. The first of the elongate pterygiophores is slightly heavier than the others and supports 2 or 3 of the anterior fin rays. It is inserted between the neural spines of vertebrae 12 and 13, or 13 and 14. The long pterygiophores are expanded dorsally, forming a more rigid support for the rays. There usually are 2 or 3 fewer pterygiophores than dorsal rays. In front of the pterygiophores of the dorsal fin there are about 12 ossified interneurals supported between the bifurcated neural spines (Pl. 7, A). The first is the largest and heaviest.

An adipose fin which does not contain any ossified elements or bony support is present.

The anal fin has from 13 to 15 rays. The first 4 or 5 of these are unbranched. The skeleton of the anal fin is similar to that of the dorsal fin, each ray supported by 3 ossifications separated by cartilage. A small distal pterygiophore lies between the two arms of each ray; an intermediate horizontal pterygiophore lies embedded in muscle between that ray and the one next posterior, and a proximal long pterygiophore, directed anterodorsally is inserted between the haemal spines (Pl. 7, B). The distal ends of the proximal elements are not expanded as in the dorsal pterygiophores. There are fewer pterygiophores than rays, the usual number being 11 or 12. The last 2 and the first 2 fin rays are supported by single pterygiophores. The first proximal pterygiophore is most often inserted between the last trunk and first caudal vertebrae.

Appendicular Skeleton

PECTORAL GIRDLE

The pectoral girdle consists of 9 paired bones which have a ligamentous attachment to the skull, dorsally, and which curve ventrally so that the cleithra lie beneath the pharynx.

POSTTEMPORAL. The pectoral girdle is attached to the cranium by the forked, posttemporal bone (Pl. 8, A and B). The posttemporal is a curved intramembranous bone which begins to ossify quite early. The dorsal fork is longer and broader than the ventral fork and almost meets its mate from the opposite side at the midline. It is attached to the epiotic by a strong ligament. The spine-like ventral fork is much shorter and smaller and is the posterior ossification of a ligament between the posttemporal and opisthotic. On the dorsal surface of the posttemporal, directly above the ventral fork is a bony tube with 2 or 3 pores which transmits the lateral canal from the extrascapular to the supracleithrum. Ventrally the posttemporal overlaps the supracleithrum.

SUPRACLEITHRUM. The supracleithrum is a concave intramembranous bone with an acute dorsal thickening which fits under the posttemporal (Pl. 8, B). Just below this, it receives the lateral canal from the posttemporal and transmits it to the lateral line. Ventrally the supracleithrum is somewhat expanded but thinner as it overlaps the cleithrum (Pl. 8).

CLEITHRUM. The cleithrum is a large, triangular intramembranous bone which comprises a considerable part of the pectoral girdle (Pl. 8). Dorsally, from a point at a level with the middle of the opercle, it curves around beneath the branchiostegal rays and forward to the level of the epihyal bone. It has a fold on its ventrolateral surface, that becomes a thickened ridge which turns inward at the scapular articulation and passes upward on the inner surface of the dorsal arm. Posteriorly the cleithrum overlaps 2 of the 3 postcleithra and, ventrally, it articulates with the scapula. Near the scapular articulation it is braced from beneath by two prongs from the mesocoracoid and by a pendant cleithral flange which joins a flange from the coracoid (Pl. 8, A). The anterior tip of the cleithrum articulates with the forward extension of the coracoid (Pl. 8, B).

POSTCLEITHRA. The grayling has 3 postcleithra which arise intramembranously. The first two are similar in size and shape, being thin ovals and more than twice as long as broad (Pl. 8). The first is partly covered by the supracleithrum and cleithrum (Pl. 8, B). Ventrally it narrowly overlaps the second postcleithrum. Posteriorly all three are buried in the skin and appear superficially almost continuous with the scales. The 2nd postcleithrum lies almost wholly beneath the cleithrum, except ventrally where it in turn overlaps the 3rd postcleithrum (Pl. 8, B). The 3rd postcleithrum is quite different from the other two. Less scale-like, it is an arched splint of bone lying in the muscle beneath the pectoral fin (Pl. 8).

SCAPULA. The primary shoulder girdle consists of the scapula, coracoid, and mesocoracoid, all endochondral bones. The scapula lies ventral of the cleithrum to which it articulates (Pl. 8, A). Anteriorly the scapula is separated from the coracoid and the upper two actinosts by a narrow strip of cartilage. The first pectoral ray articulates with the posterior border of the scapula. A mesally directed ridge of bone from its ventral edge articulates with one of the projections on the mesocoracoid. The large scapular foramen lies wholly within the scapula (Pl. 8).

MESOCORACOID. The mesocoracoid is a strongly arched, inverted, U-shaped bone which lies on the mesial surface of the girdle and acts mainly as a brace between the cleithrum and the primary shoulder girdle (Pl. 8, A). The outer arm is narrow and splint-like and lies in intimate contact with the inner wall of the cleithrum, extending downward almost to the cartilaginous edge of the scapula. The inner arm is greatly expanded and longer; it articulates broadly with a mesiodorsal flange from the coracoid and with the inner edge of the scapula. Thus is formed the large mesocoracoid arch (Pl. 8).

CORACOID. The coracoid is keel-shaped with two dorsally directed wings of bone, an inner, meeting the mesocoracoid, and an outer, meeting a flange from the cleithrum (Pl. 8, A). Posteriorly the coracoid is separated from the scapula by a narrow strip of cartilage below which a pointed posterior process extends backward (Pl. 8). The coracoid extends forward beneath the cleithrum, its anterior tip turning upward to meet the anterior end of that bone. An oval interosseous space (Starks, 1930) is left separating the coracoid and cleithrum between their two points of union (Pl. 8, A and B).

PECTORAL FIN. Four actinosts are present, the upper two articulating with the scapula and the lower two with a triangular piece of cartilage lying between the coracoid and scapula. The upper is the smallest; the others become progressively longer ventrally (Pl. 8, A and B). There are 15 to 17 pectoral rays. The uppermost ray is longest and heaviest, and articulates directly with the scapula. The remainder become progressively smaller, ventrally, and articulate with the actinosts.

PELVIC GIRDLE

The pelvic girdle consists of a pair of L-shaped bones, the basipterygia (Pl. 7, D). The foot of the L is situated posteriorly and directed medially, meeting its mate from the opposite side in a cartilaginous articulation at the midline. The longer, anteriorly-directed arm meets its fellow at the midline in a knob of cartilage. Thus the pair encloses a large interosseous triangle (Pl. 7, D). On the posterior surface of each basipterygium there is a small ossification (pterygiophore) lying between the basipterygium and the most medial fin ray. The rays are paired, each forking on either side of the basipterygium, on the outer curved portion of which they articulate. There are usually 11 rays in the pelvic fin, of which 9 or 10 are branched; the outer 1 or 2 are short and simple. An axillary process or modified scale lies along the outer angle of the pelvic fin.

OSTEOLOGY OF THE WHITEFISHES (COREGONINAE)

The whitefishes may be separated from other salmonid fishes by the presence of a well-ossified hypethmoid bone and the lack of teeth on the maxillae at any stage in life. Three genera may be recognized in this subfamily: *Prosopium*, *Stenodus*, and *Coregonus*. *Prosopium* is distinguished from the other two by a single flap between the nostrils (two in *Coregonus* and *Stenodus*), an ossified basi-branchial plate (Pl. 6, A) superimposed over the median basibranchial bones (also present in the Salmoninae but absent in *Stenodus*, *Coregonus*, and *Thymallus*), and, in so far as is known, parr marks on the juveniles. *Prosopium* includes 6 species: *cylindraceum*, *williamsoni*, *spilonotus*, *abyssicola*, *coulteri*, and *gemmiferum*. Of these, the first inhabits eastern Asia and northern North America, the others all live in western North America and *P. coulteri* also occurs in Lake Superior.

Stenodus is characterized by having a closed orbital ring (supraorbital one meets the dermosphenotic above the orbit), a large, well-toothed mouth in the adult, and large, heavy bones. There is a single species, *S. leucichthys*, inhabiting the Caspian region, eastern Asia and northwestern North America.

In *Coregonus* there are two internarial flaps, no ossified basibranchial plate, the orbital ring is open dorsally, the mouth is small to moderate in size with weak to moderate dentition, and parr marks are never present. Differences in structure and position of mouth, body form, and number and length of gill rakers have been used by some authors to separate some species as a genus (*Leucichthys* or *Argyrosomus*) distinct from *Coregonus*. These characters are subject to broad intergradation and overlap among species (e.g., Svärdson, 1957). Similar modifications have evolved independently in *Prosopium* as apparent adaptations to feeding behavior, and those in *Coregonus* may well have developed repeatedly (Drs Bailey and Eschmeyer, personal communication). I did not find any distinctive morphological differences and thus *Leucichthys* is regarded as unacceptable and is placed in the synonymy of *Coregonus*. The species of *Coregonus* range throughout northern Europe and Asia and northern and northeastern North America. The number of species to be recognized in *Coregonus* is a subject for debate. Berg (1948) listed 11 from Russia alone but Svärdson (1957) believes there are only 7 in the entire Palearctic. Five species are endemic to the Great Lakes (*alpenae*, *hoyi*, *johannae*, *kiyi*, and *reighardi*) and 5 additional species (*artedii*, *clupeaformis*, *nigripinnis*, *nipigon*, and *zenithicus*) inhabit those waters but occur, or are thought to occur, elsewhere to the northwest. Four other species *sardinella* = *albula* (Svärdson, 1957), *autumnalis* = *oxyrhynchus* (Svärdson, 1957), *nasus*, and *pidschian* are known from northwestern North America but all of these occur also in Siberia and two are perhaps conspecific with species living in the Great Lakes, as suggested by Svärdson (1957). The remaining species *lavaretus*, *peled* and *baunti* inhabit northern Europe and Asia. If Svärdson's estimate of the number of Old World species is correct, there may be as few as 15 species of *Coregonus*, probably not more than 17.

Only adult specimens of *Stenodus* were available. All data on *Prosopium* were obtained from preserved material; all six species were used in making the comparisons. Species of *Coregonus* were more readily accessible in both fresh and preserved state (Table I).

The Chondrocranium

THE OLFATORY REGION

The general shape of the coregonine olfactory region is similar to that of the grayling, there being a bluntly rounded rostrum and two lateral horns forming the margin of the nasal cup. The region also is greatly expanded in width, posteriorly, as it flares out into the prefrontals. However, the prefrontals are directed forward, especially in *Coregonus artedii* (Pl. 3, A) rather than at right angles to the ethmoid cartilage, as in the grayling (Pl. 1, A). The primary distinction is in the endochondral ossification, the hypethmoid lies dorsally between the nasal capsules so that in the coregonine fishes the cartilaginous nasal capsule is partly ossified (Pl. 3, A). A further difference is noted in *Prosopium cylindraceum*, *P. abyssicola*, *P. williamsoni*, *Coregonus nasus*, and to a less extent in *C. clupearformis*, in which the rostrum curves ventrally. The whole anterior ethmoid region is rounded so that the rostral horns lie ventral to the nasal capsules. Berg (1940: 426) stated that the hypethmoid of *Stenodus leucichthys* is a thin round plate which does not penetrate deep into the cartilage. My observations indicate the only difference to be that in *Stenodus* the dorsal plate is rounded, rather than rectangular or bifurcated as in other coregonines.

THE ORBITAL REGION

As in the grayling, much of the orbital region in the Coregoninae has been eliminated. Three bones comprise the orbital region, the orbitosphenoid, a pair of pterospheneids, and the basisphenoid. The orbitosphenoid, which is absent in the grayling, is a small wing-shaped endochondral bone in *Prosopium* and *Coregonus*, but is large and heavy in *Stenodus*. It lies in the sagittal plane and forms part of the dorsal interorbital septum. The orbitosphenoid is surrounded by cartilage, except posteriorly where it meets the pterospheneid. The pterospheneids form part of the posterior wall of the orbit, then extend dorsally to form part of the rim of the dorsal fontanelles (Pl. 3, A). The small Y-shaped basisphenoid touches the prootics on either side with the leg extending anteroventrally to connect to the parasphenoid by a band of cartilage. The basisphenoid is poorly developed in the coregonine fishes. It is much smaller than in the grayling and is often incompletely ossified. It is difficult to find and is most readily located in stained specimens. It was not located in all specimens; thus it may have been overlooked or at times it may fail to ossify. However, a basisphenoid was found in some specimens of *Coregonus artedii*, *C. hoyi*, *C. clupearformis*, *Prosopium cylindraceum*, *P. gemmiferum*, *P. williamsoni*, and *Stenodus leucichthys*. The basisphenoid may be present or absent in the coregonines (Berg, 1940: 426).

THE OTIC REGION

All 8 bones (6 are paired) found in the otic region of the grayling are present in the chondrocranium of the coregonines, and marked similarity in form and position is observed throughout. These 8 bones are the paired sphenotics (Pl. 3, A), prootics, pterotics, epiotics, opisthotics, and exoccipitals. The median bones are the supraoccipital (Pl. 3, A) and the basioccipital. The opisthotic is present in all coregonines; it rests loosely at the junction of the exoccipital, pterotic, and epiotic (Pl. 3, A). The supraoccipital is a rounded median bone and, except for its posteriorly directed spine, is almost completely covered by the parietals. The curved exoccipital forms part of the posterior and lateral wall of the chondrocranium. It is the only bone in contact with the foramen magnum. The main articulation for the first vertebra is the basioccipital, which then extends forward beneath the chondrocranium to meet the prootic.

Three otoliths are present in the coregonines but only the largest, the sagitta, was studied. As in the grayling, it lies in a vault on the floor of the basioccipital, with the anterior rostrum pointing toward the prootic. The sagitta is similar among the coregonines examined and is much like that of the grayling (Pl. 16).

Investing Bones

DORSAL ROOFING BONES

The head of the Coregoninae is not so completely overlain with dermal bone as is that of the grayling; the bones are thinner and more transparent (except in *Stenodus*). All dorsal roofing bones present in the grayling also are present in the coregonines and some, such as the paired nasal and pterotic and the median supraoccipital crest, do not show sufficiently important differences to be contrasted.

The dorsal roofing bones of the coregonines form a rather acute angle, anteriorly (Pl. 9, C). Thus, the supraethmoid and premaxillae (except in *Stenodus*) are small and narrow. The supraethmoid covers the ethmoid cartilage and at least part of the hypethmoid. In those species with subterminal mouths (*Coregonus clupeaformis*, *C. nasus*, *Prosopium abyssicola*, *P. cylindraceum*, *P. spilonotus*, and *P. williamsoni*) the supraethmoid overlaps only a small portion of the anterior end of the hypethmoid. In the above species, it appears that the supraethmoid follows the rounded curvature of the snout while the hypethmoid remains stationary. Since the supraethmoid appears to have moved forward around the snout, it is not in contact with the frontals as in *Stenodus leucichthys*, *Prosopium gemmiferum*, *Coregonus sardinella*, *C. artedii*, and similar forms with terminal mouths. Anteriorly the supraethmoid forms a nearly straight suture with the premaxillae at the midline (except in *Coregonus clupeaformis* and *C. nasus*). In these two species, the supraethmoid has a median, vertical ridge of bone at its pointed anterior end. This is similar to that illustrated by Berg (1940: 237) for *Coregonus lavaretus*, but the position is somewhat different since the supraethmoid lies anterior of the hypethmoid in *C. clupeaformis* rather than over it, as is shown for *C. lavaretus*. Of the dorsal roofing bones, the supraethmoid

shows the greatest diversity among the coregonine fishes. In *Stenodus leucichthys*, this bone is large, but it is thin, flat, and digitate posteriorly (Pl. 11). The closest approach to this type in other coregonine species is found in *Coregonus artedii* and allied species, in which it is much smaller but is thin, flat and somewhat emarginate posteriorly (Pl. 12, B). In *Prosopium* (except *P. gemmiferum*) the supraethmoid is somewhat concave and with very few irregularities at either end (Pl. 12, C and D). It is proportionately longer, being about 3 times as long as wide, as compared with the 2 to 1 ratio found in *Coregonus*. In *Prosopium gemmiferum*, the supraethmoid is long, narrow and covers much of the underlying hypethmoid bone (Pl. 12, G) and although it is a larger bone it is not much different in appearance from that of *P. abyssicola* (Pl. 12, D). Its greatest length-to-width ratio is about 4 to 1, thus confirming the interpretation of affinity with *Prosopium* rather than *Coregonus*. The supraethmoid of *Coregonus nasus* and *C. clupearformis* (Pl. 12, A) is also distinctive. It is triangular, with 3 posteriorly directed points and the length-to-width ratio is about 2 to 1. It probably indicates an independent evolutionary line from *Prosopium*, although both genera have curved snouts and inferior mouths. In *Coregonus sardinella*, the posterior margin of the supraethmoid (Pl. 12, E) is not deeply notched as in *C. artedii* (Pl. 12, B), *C. kiyi*, *C. reighardi* and related forms. However, it is rather broad and flat as it is in these species.

As in the grayling, the frontals of the coregonine fishes are large subtriangular bones covering most of the dorsal surface of the chondrocranium (Pl. 9, C). In *Stenodus leucichthys*, supraorbital 1 meets the long, anteriorly-directed dermosphenotic, preventing the frontal from being exposed on the dorsal rim of the orbit. The exclusion of the frontal from the orbital rim is approached in *Coregonus*; the condition differs among its various species, but the frontal forms about 10 to 15% of the circumference of the orbit. In species of *Prosopium*, the frontal occupies about 20 to 25% of the orbital rim, and *Thymallus arcticus* is intermediate, with a break of about 17% of the orbital ring. Most of the posterior margin of the frontals overlaps the parietals. The frontals meet at the midline, posteriorly, but gradually separate toward the snout. The frontal in *Coregonus artedii* and in *Stenodus leucichthys* is a rather long, tapered bone whereas that of *Prosopium cylindraceum* and of *P. williamsoni* is somewhat rounded laterally, shorter and comes abruptly to a point anteriorly. In *Coregonus clupearformis* and *Prosopium gemmiferum* the frontals are somewhat intermediate between these two shapes.

The parietals are irregularly-shaped bones which usually cover a small part of the dorsal fontanelles and much of the supraoccipital. The posterior margins of the parietals are hidden by the dorsal extrascapular bones (Pl. 9, C). The parietals meet in the midline to some extent, except in *Stenodus leucichthys*, in which they are narrowly in contact or are close to the midline and are not pushed aside as in the salmonines. The parietal suture is most apparent in the species of *Prosopium*; in *Coregonus clupearformis*, the parietals are slightly separated for most of their length.

Posterior of the parietals two pairs of extrascapular bones lie across the rear margin of the skull. They are tubular and bear the supratemporal canal. The

more lateral extrascapular is the larger, being somewhat expanded posteriorly, and bears a triradiate canal. It receives two canals, the lateral canal from the pterotic and the supratemporal canal from the dorsal extrascapular, which unite and continue to the posttemporal. The more dorsal extrascapular is smaller and more slender than the other. It meets its mate from the opposite side but does not cross the midline as in *Thymallus arcticus*. The paired extrascapulars are quite stable throughout the coregonines. Two individual variations were found in *Prosopium cylindraceum*; in each specimen a third, small pair of extrascapulars was found between the other two.

Other dermal bones seen from a dorsal aspect are the premaxillae, supra-orbitals, dermosphenotics, pterotics, posttemporals, and supraoccipital. The first three are discussed with the lateral skull bones. The posttemporal is part of the pectoral girdle. The pterotics and supraoccipital are of mixed derivation. Only their dermal portions are pertinent here, and these have been mentioned.

LATERAL SKULL BONES

The lateral surface of the head of the coregonine fishes is fairly well invested with bone, except for areas around the orbit, between the postorbitals and preopercle, and above and below the pterotic (Pl. 10, A).

In some species (e.g. *Coregonus clupeaformis*, *Prosopium coulteri*, and *P. cylindraceum*) the premaxillae project; in *Prosopium gemmiferum*, *Coregonus artedii* and some others, they are about equal with the dentary; whereas in *Stenodus leucichthys* and *Coregonus alpenae* they do not extend forward as far as the dentary.

The coregonine premaxilla is a small, thin bone which meets the supraethmoid dorsally, the maxilla laterally, and its mate at the midline. In specimens of *Prosopium coulteri*, *P. cylindraceum*, *Coregonus artedii*, and *C. clupeaformis* 30 to 40 mm total length, 6 to 8 small but well-developed teeth are present. Even in later stages (73 to 84 mm total length) teeth were still clearly evident. In the adult of *Coregonus artedii* an occasional small, weak tooth may be found. A few teeth are always present on the premaxilla of the adult of *Stenodus leucichthys* (Pl. 13, F), although it is a small, narrow bone contributing little to the margin of the gape. In *Coregonus clupeaformis*, *Prosopium cylindraceum*, (Pl. 13, E) *P. coulteri*, and *P. sibilonotus*, the premaxilla is an almost vertical plate at the end of the snout, its height subequal to its length. In *Coregonus artedii* and *C. sardinella* (Pl. 13, G), the premaxilla extends so far laterally that its horizontal length is about twice its height.

The coregonine maxilla is a distinctive bone (Pl. 10, A). Instead of being long, narrow and toothed as in the salmonines and thymallines, it is short, broad and curved much like the runner on a sleigh (Pl. 13, A, B, E-G). The outstanding feature, however, is the absence of teeth at any stage of development. The maxilla also displays notable variation in shape among the whitefishes (Gasowska, 1960). In *Prosopium abyssicola*, *P. cylindraceum* (Pl. 13, E), *Coregonus clupeaformis*, and *C. nasus* (Pl. 13, A) it is S-shaped and the posterior

half is expanded. When the mouth is open, it is the middle one-third which is exposed at the margin of the gape. In *Prosopium gemmiferum* (Pl. 13, B), *Coregonus artedii*, *C. sardinella*, (Pl. 13, G) and *Stenodus leucichthys* (Pl. 13, F) the maxilla is about equally expanded throughout (except the rounded knob which articulates with the palatine) and the anterior two-thirds borders the gape when the mouth is open.

An anterior depression in the ventral margin of the maxilla, that forms the articulating surface for the premaxilla, is balanced in the rear by a dorsal depression which receives the supramaxilla. The supramaxilla is quite characteristic in the coregonine fishes, but in all there is a severely attenuate anterior projection. This is quite different from the supramaxilla in other salmonid fishes, in which this bone is a simple, lanceolate structure (Pl. 13, C-D, and H).

The first supraorbital bone is much larger in *Coregonus artedii*, *C. clupeaformis*, and *Stenodus leucichthys* than in the grayling. In these 3 species, the first supraorbital is one-third to one-half the length of the frontal, but in the grayling it is always less than one-third the frontal length. In *Prosopium* it is a small bone, as in the grayling. The greatest development is shown in *Stenodus leucichthys*, in which the supraorbital extends backward until it touches the dermosphenotic, eliminating the frontal from the rim of the orbit.

The second supraorbital is a narrow, curved bone that is much smaller than the first and not so strongly arched as in the grayling. It has a broad ventral suture with the lachrymal but it barely makes contact by a dorsally upturned point with supraorbital one.

The lachrymal, 3rd in the series of circumorbital bones, is thin, more or less triangular, and bears the anterior terminus of the infraorbital canal. The anterior end of the lachrymal is bluntly rounded, more so in *Stenodus leucichthys* than in any other coregonine. Posteriorly it meets the infraorbital, which exhibits little difference among the various species studied.

There are 3 postorbital bones in all species of coregonines studied. The first is somewhat narrower anteriorly where it meets the infraorbital, and widens dorsally at its suture with the 2nd postorbital. Postorbital 3 articulates with the dermosphenotic. All three carry the infraorbital canal. In all but *Stenodus leucichthys*, the 3rd postorbital is widest; but in that species the 2nd is the broadest. Also, in *Stenodus* the postorbitals fail by a considerable space to extend to the preopercle. In species of *Prosopium*, only the 3rd postorbital comes in contact with the preopercle. In *Coregonus*, the 3rd and usually a part of the 2nd postorbital are in narrow contact with the preopercle (Pl. 10, A).

The dermosphenotic is the 8th circumorbital bone in the coregonine fishes. Like the grayling, it bears a triradiate sensory canal. It lies over the sphenotic, articulates with postorbital 3 ventrally, with the frontal dorsally (except in *Stenodus*) and with the pterotic laterally. The dermosphenotic forms part of the posterodorsal rim of the orbit. In *Stenodus* the bone is produced anteriorly and contributes a larger share to the orbital rim; it meets the 1st supraorbital to close the circumorbital ring.

The V-shaped dentary is a concave bone forming the greater part of the lower jaw. Anteriorly it curves inward to meet the dentary of the opposite side in a loose, easily separable symphysis. The longer lower arm of the V is almost straight along its ventral surface and bears the mandibular canal. At its posterior tip, it just touches the small retroarticular, and the angular fits between the two arms of the V. The dorsal arm of the V is wing-shaped and gives the coregonine dentary its characteristic shape, which is readily distinguishable from the grayling's dentary. The anterodorsal slope of this wing is rather abrupt in small-mouthed species (*Coregonus clupeaformis*, *C. nasus*, *Prosopium coulteri*, *P. cylindraceum*, and *P. williamsoni*), more gradual in the larger-mouthed forms (*Coregonus artedii*, *C. hoyi*, *C. kiyi*, *Prosopium gemmiferum*, and *Stenodus leucichthys*). The inner concavity of the dentary receives the anterior tip of Meckel's cartilage. Although teeth are borne on the dentaries of the juveniles of all species studied (to a length of approximately 80 mm), only *Stenodus leucichthys* bears teeth as an adult, and these are few and weak (Pl. 11). Berg (1940: 426) mentioned that a small inframandibular bone is present on the dorsal wing of the dentary in *Stenodus leucichthys*. However, this bone was not noted in the specimens of *Stenodus* used in this study (Pl. 11). Dineen and Stokely (1954) pointed out that the inframandibular bone is not a constant feature in *Umbra limi*, a characteristic which may apply also to *Stenodus*.

Except for the posterior articular portion, most of the coregonine angular is a thin transparent bone fitting into the V-shaped notch in the dentary. Its posterodorsal surface has a curved notch to receive the rounded knob of the quadrate. Just below this notch a tubular bone has fused to the angular, providing a connection from the preopercular to the mandibular canal. Ventral to the canal, there is an irregular suture with the retroarticular. The inner posterior surface of the angular is well ossified around Meckel's cartilage. The mandibular portion of the adductor mandibularis muscle is firmly inserted along the mesal surface of Meckel's cartilage, as well as on the coronomeckelian. The angular of *Coregonus artedii* and *Prosopium gemmiferum* is long and pointed, anteriorly, much like that of *Thymallus arcticus*. In *Stenodus* the angular is rounded anteriorly, and in *Coregonus clupeaformis*, *Prosopium cylindraceum* and *P. williamsoni* it is pyramidal in form with an S-shaped curve in front.

The retroarticular, a small triangular bone at the posteroventral corner of the angular, is little differentiated among the species studied and is similar to the retroarticular of the grayling, except that it is slightly larger and is not firmly fused to the angular. All of the coregonine fishes studied possess a coronomeckelian lying partly over Meckel's cartilage and fused to the angular.

The coregonine preopercle is a strongly arched bone, similar to that of the grayling. The vertical arm is about $1\frac{1}{2}$ times the length of the horizontal arm and carries the sensory canal directly to the pterotic, where it joins the lateral temporal canal. No suprapreopercular bone is present in any of the Coregoninae (Pl. 10, A).

Paired opercles, subopercles, and interopercles are present but no significant differences were noted among the various species of coregonines studied.

The branchiostegal rays lie in a series on the ventral surface of the head, each overlapped by the one next behind. The first 5, 6, or 7 rays are attached to the ceratohyal; the remainder to the epihyal bone. The number of branchiostegal rays varies from 6 to 11. *Coregonus artedii*, *C. hoyi*, *C. kiyi*, *Prosopium gemmiferum* and *P. williamsoni* have 7 to 9 branchiostegals; *C. clupearformis* has 8 to 10; *P. coulteri* has 7 or 8 and *P. cylindraceum* has 6 to 8. *Stenodus leucichthys* has 10 or 11 branchiostegal rays, the largest number in the Coregoninae.

VENTRAL BONES OF CRANIUM

The vomer in the coregonines is a thin, rounded bone lying on the ventral surface of the ethmoid. In *Stenodus leucichthys* it is well developed and the head bears numerous small teeth (Pl. 11). It narrows posteriorly, to a point which overlaps the parasphenoid. In *Coregonus artedii* and *C. clupearformis*, the vomer is smaller and has a few vestigial teeth only in the young. It is widest anteriorly, does not extend far back, and terminates in a blunt tip. In the species of *Prosopium*, the vomer is poorly developed; there remains a small oval ossification and a short shaft which barely touches the parasphenoid. No teeth were observed. Except in *Stenodus*, the vomer of the coregonine fishes is less well developed than in *Thymallus*.

The parasphenoid extends almost the entire length of the chondrocranium, from the lateral horns of the rostrum to the rear end of the basioccipital. In all species it is overlapped anteriorly by the vomer, but to a greater extent in *Coregonus artedii*, *C. clupearformis*, and *Stenodus leucichthys*. Just behind the orbit, two wings from the parasphenoid extend dorsally to meet the basioccipital and enclose the posterior myodome. This chamber for the eye muscles is open posteriorly in all the coregonines. In *Coregonus artedii*, the parasphenoid is fairly straight until it reaches the otic region and then bends dorsally, the two parts forming an angle of about 160°. This is similar to but less abruptly bent than that of the grayling, which has an angle of about 140°, and *C. clupearformis* with about 150°. In *Prosopium cylindraceum*, the bending is still less pronounced (about 170°), and in *Stenodus* the ventral contour of the parasphenoid is straight (approximately 180°).

Visceral Arches

PALATOQUADRATE ARCH

The palatine in the Coregoninae is rather short and lies in front of the ectopterygoid. The anterior endochondral portion is cylindrical and thus is well differentiated from the posterior dermal portion. The palatine articulates at two points with the ethmoid cartilage, the first beneath the anterior tip of the maxilla and the second a short distance posterior. The second articulating surface is particularly well developed in the coregonines, ending in a rounded, well-ossified cylinder. Beyond this point, the palatine becomes much reduced in size and ends rather abruptly, especially so in the species of *Prosopium*. Weak, small teeth are borne on the palatine during the young stages of all coregonines.

studied, but they are lost as juveniles, except in *Stenodus leucichthys* and *Coregonus sardinella*. In adults of *Stenodus* there are many small teeth in a broad band that is continuous with the vomerine tooth patch (Pl. 11).

Paired ectopterygoids, quadrates, metapterygoids, and mesopterygoids are present in all coregonines. The mesopterygoid is never toothed in the coregonines.

HYOID ARCH

The hyomandibular of the coregonines is similar in shape to that described for *Thymallus arcticus*. Among the coregonines, the hyomandibular of *Stenodus leucichthys* shows the greatest divergence. The bone is relatively shorter than in other species and the opercular condyle is somewhat longer.

The symplectic acts as a connecting rod of bone between the quadrate, hyomandibular, and metapterygoid. The interhyal articulates at the cartilaginous junction of the symplectic with the hyomandibular. There is little difference among the symplectics of the various species studied.

The description of the interhyals, epihyals, ceratohyals, and hypohyals of the grayling suffices for the coregonines, as there is little distinctive about these bones in the subfamily. Two or 3 branchiostegal rays are borne on the epihyal, the remainder on the ceratohyal.

The basihyal is cartilaginous and covered with a lingual plate. In the grayling the lingual plate is spatula-shaped, with a patch of teeth in the centre (Pl. 6, C). However, in *Coregonus artedii* and *C. sardinella* the lingual plate is long and thin with weak teeth scattered along the length of the bone. In *Stenodus leucichthys* it is of similar shape but fairly bristles with tiny teeth and overlaps the first basibranchial. The lingual plate of *Coregonus clupeaformis* and *C. nasus* is oval and many small teeth are scattered over the dorsal surface. It overlaps the first basibranchial bone in *C. nasus* but not in *C. clupeaformis* (Pl. 6, D). The lingual plate is more variable in *Prosopium*. In *P. coulteri* and *P. gemmiferum* it does not touch the first basibranchial. A well-developed central patch of teeth is present on the oval lingual plate of *P. coulteri*, but teeth are absent from the somewhat longer bone of *P. gemmiferum*. In *P. abyssicola*, *P. spilonotus*, *P. cylindraceum*, and *P. williamsoni* a small central patch of teeth is present and the lingual plate touches the first basibranchial. In the first two of these 4 species the shape is ovate; in the last two it is elongate (Pl. 6, A).

BRANCHIAL ARCHES

Three pairs of ossified pharyngobranchials are present in the coregonines, the first of which articulates with the parasphenoid. As in the grayling, they articulate with each other and with the epibranchials. One to 4 small gill rakers usually are present on the anterior edge of the 2nd and 3rd pharyngobranchials. A pharyngeal plate lies over the 3rd pharyngobranchial. It is small and bears a few weak teeth in *Coregonus* and *Prosopium* (Pl. 6, A and D). It is larger and the teeth are well developed in *Stenodus*.

Four pairs of epibranchials are present. The 4th is atypical, with a round

expanded posterior portion which is partially covered by a 2nd pharyngeal plate. The 2nd plate lies on the dorsal surface of the epibranchial near its junction with the pharyngobranchial, and bears a cluster of tiny teeth (Pl. 6, A and D). Gill rakers are found on the anterior edge of all 4 epibranchials and also on the posterior edge of the first 3.

There are 5 pairs of ceratobranchials. The 5th is somewhat expanded and bears a 3rd, toothed pharyngeal plate (Pl. 6, A and D). As in the grayling, gill rakers are borne on the anterior surface of all 5 bones and on the posterior edge of the first 4. The rakers on the posterior side of the 1st ceratobranchial in *Stenodus* are few and tiny.

Three pairs of hypobranchials, similar to those in the grayling connect the ceratobranchials with the basibranchials. The first 2 hypobranchials bear gill rakers on both anterior and posterior surfaces; the 3rd is cone-shaped and bears rakers on only the anterior side in *Coregonus* and *Stenodus*. All species of *Prosopium* (including *gemmiferum*) are like *Thymallus arcticus* in having rakers on only the anterior edge of the hypobranchials.

There are 4 basibranchial bones which lie in a series and are separated by cartilage, although the cartilaginous bridge between the 1st and 2nd is very narrow. The 1st basibranchial is shorter than the others and is triangular. It articulates with the basihyal anteriorly. In *Prosopium*, a single, long, narrow basibranchial plate is present, lying over the dorsal surface of the posterior half of the 2nd basibranchial and extending backward to above the anterior half of the 4th basibranchial (Pl. 6, A). As in *Salmo trutta caspius* (Tchernavin, 1938b), it is fused to the 3rd basibranchial. The basibranchial plate is not present in the grayling, in *Stenodus*, or in any of the species of *Coregonus* examined. It is present in *Prosopium abyssicola*, *P. coulteri*, *P. cylindraceum*, *P. gemmiferum*, *P. spilonotus*, and *P. williamsoni*.

The branchial skeleton of *Stenodus leucichthys* is more dentigerous than that of the other coregonines. Minute teeth are found embedded in the skin over all 3 pairs of pharyngobranchials, on the 4 pairs of epibranchials and along the entire length of both the anterior and the posterior copula. Teeth also are attached to the dermal plates (the lingual and the 3 pairs of pharyngeal plates).

UROHYAL

A urohyal bone is present in all coregonines but it is not particularly distinctive. It is rather flat, ventrally, with a dorsal crest as in the grayling.

Axial Skeleton

VERTEBRAL COLUMN

The vertebral column of the whitefishes ranges from a low of 52 vertebrae in *Prosopium coulteri*, to a high of 69 vertebrae in *Stenodus leucichthys* (Koelz, 1929: 321; Eschmeyer and Bailey, 1955: 172; Fuller, 1955: 771). The vertebrae have essentially the same shape as in the grayling. They are largest in the median part of the trunk, becoming progressively smaller anteriorly and posteriorly.

The neural arches are prolonged dorsally into neural spines. The anterior spines are separated to a point below the dorsal fin. They then fuse into sharp spines which slant backward toward the caudal fin. The last 2 or 3 neural spines are expanded. Epineurals are borne on the lateral surfaces of the first 28 to 38 neural arches, the lower numbers being found in species with fewer vertebrae. Occasionally the atlas does not bear an epineural. Anteriorly the neural arches are recessed in pits in the middle part of the centrum, but behind the dorsal fin they are fused to the anterior part of the centrum. Ventrolaterally, pairs of transverse processes are set into pits in the centra. The pleural ribs articulate with the outer surface of the transverse processes. Beyond the dorsal fin, the transverse processes gradually become smaller and fuse to the centra. As in the grayling, the transverse processes of the posterior 7 or 8 trunk (precaudal) vertebrae are longer and slant backward, and the final 2 or 3 are fused across the midline to form a haemal canal. The 1st vertebra does not have ribs but the remaining trunk vertebrae bear pairs of pleural ribs. Those belonging to the precaudal vertebrae do not have articular surfaces but rather adhere tightly to the posterior surface of the transverse processes. The last 20 to 24 caudal vertebrae bear posteriorly directed haemal spines, and the final 3 or 4 of these are broad and flat. Epipleurals, such as are present in the grayling were not observed in any of the Coregoninae.

The caudal fin of the whitefishes is like that of the grayling, with 3 upturned vertebrae and a cartilaginous urostyle. The neural spine of the 4th vertebra from the last, slants sharply backward and looks very much like an epural, similar to the same condition in the grayling (Pl. 14, G and H). It is not fused to its neural arch as are the more anterior neural spines. Two epurals (3, if the detached neural spine from the 4th last vertebra be included) are present in all the coregonines observed. Three pairs of uroneurals are present. The 1st (most anterior) uroneural is a large plate-like structure extending over the last 3 or 4 vertebrae and onto the urostyle. As in the grayling, it has only a small dorsal crest (Pl. 14, G and H). The 2nd lies dorsolaterally of the 1st, partly covering the 1st uroneural and the urostyle. The 3rd and smallest lies beside the second uroneural but extends more posteriorly. The coregonines have 7 hypurals in the caudal fin. Like that in the grayling, the 2nd hypural is the largest. The urostyle curves sharply dorsad and ends between the paired bases of the caudal rays (Pl. 14, G and H). Although the urostyle is chiefly cartilaginous, 1 or 2 nodules of bone may be present.

The principal rays of the caudal fin are typically 19 (17 branched) in number in all the whitefishes studied.

MEDIAN FINS

The dorsal fin of the whitefishes is very similar to that of the grayling, except that the rays are fewer. The anterior 2 to 4 rays are unbranched, the remainder are branched but the rays are shorter. All are supported by a series of 3 pterygiophores, exactly as described for the grayling. The insertion of the most

anterior pterygiophore is somewhat variable; it may be anywhere behind the neural spine of any vertebra from 12 to 17. This variation is true of all coregonines except *Stenodus*, in which the dorsal fin is located somewhat posteriorly, and the 1st pterygiophore lies behind vertebra 20, 21, or 22. From 12 to 16 flat inter-neurals lie in the muscle anteriorly of the dorsal fin. The largest of this series is borne just behind the skull and the smallest is next to the dorsal fin.

The number of dorsal rays is quite variable, between 10 and 15, and is not a particularly valuable taxonomic character in the whitefishes. This figure is somewhat higher than that reported by Koelz (1929) who counted a low of 7 rays in *C. hoyi*, but Eschmeyer and Bailey (1955: 163) pointed out that Koelz did not count the short, anterior unbranched rays. Minimum figures usually are characteristic of *Prosopium coulteri* and maximum counts most often are encountered in *Stenodus leucichthys*. Therefore, the dorsal ray count of *Stenodus* most closely approaches, but does not reach, the minimum number (17) in *Thymallus*.

The coregonine anal fin is basically similar to the dorsal fin. The insertion of the anterior pterygiophore again is variable, and may lie from between vertebrae 29 and 30 to between 42 and 43. The lower figure is that found in *Prosopium coulteri*, while the larger is characteristic of *P. cylindraceum* and *Stenodus leucichthys*, but there is overlap between these extremes. The number of anal fin rays varies from 11 to 16. Again, this figure is higher than that given by Koelz (1929) who omitted short rays from his counts. The higher count is characteristic of *Stenodus*, whereas several species (*Coregonus artedii*, *C. alpenae*, and *P. coulteri*) may have as few as 11 anal rays.

Appendicular Skeleton

PECTORAL GIRDLE

As in the grayling, the posttemporal bone in the Coregoninae connects the pectoral girdle to the dorsal part of the skull at two points, one with the epiotic and the other with the opisthotic bone. The ventral portion of the posttemporal is more expanded than in *Thymallus*. The supracleithrum is the 2nd bone of the series and transmits the lateral canal to the lateral line. Ventrally, the supracleithrum overlaps the cleithrum and 1st postcleithrum. The whitefish cleithrum, like that of the grayling, is the largest bone of the pectoral girdle and extends far forward beneath the pharynx.

Three postcleithra are present in all the coregonines studied. Berg (1940) stated that *Stenodus leucichthys* has only 2 postcleithra, but 3 were found in each of the 8 specimens examined (Pl. 11). The 3rd postcleithrum is small and rounded, in contrast to the long, narrow, splint-like bone in other coregonines. It seems clear that the 3rd postcleithrum was overlooked by Berg. The oval 1st postcleithrum lies below the angular junction of the supracleithrum and cleithrum and is overlapped by these 2 bones. There is a moderate gap of variable width between the 1st and 2nd postcleithrum in *Stenodus* (Pl. 11) and

in *Coregonus*, and a narrow space between them in *Prosopium*, but these 2 postcleithra are in contact in the grayling (Pl. 8, A). The 2nd postcleithrum is the largest bone of the series and is almost completely covered by the posterior expansion of the cleithrum, which in turn overlaps the 3rd postcleithrum. The latter is a narrow bone, somewhat expanded dorsally but most often coming to a sharp point ventrally. It is subject to individual variation and often is quite blunt and oblong in *Coregonus artedii*, and it is round or oval in *Stenodus* (Pl. 11).

The bones of the primary shoulder girdle consist of paired scapulae, mesocoracoids, and coracoids. These in coregonines are similar in shape and position to those described for the grayling. The scapular foramen lies wholly within the scapula, the mesocoracoid is arched, and the coracoid runs forward, and meets the coracoid from the opposite side where they articulate with the cleithra.

Four actinosts are present in all the whitefishes studied. They support all but the 1st pectoral fin ray, which articulates directly with the scapula.

The number of pectoral rays ranges from 13 to 18 among the coregonines (Koelz, 1929: 319), but the number is not distinctive, there being broad overlap among species. *Coregonus artedii*, *C. hoyi*, *C. kiyi* have a relatively high count, 14 to 18 rays, species of *Prosopium* have 13 to 16, and other coregonines have 14 to 18 rays.

PELVIC GIRDLE

Like the grayling, the whitefish pelvic girdle consists of a pair of L-shaped basiopterygia which meet anteriorly in a rather sharp point. Posteriorly they join at the midline in a cartilaginous suture. The pelvic fin rays range in number from 9 to 13, but their number is of little taxonomic value (Koelz, 1929: 320; Eschmeyer and Bailey, 1955: 170). A well developed axillary process is found in all coregonines.

OSTEOLOGY OF THE TROUTS (SALMONINAE)

The Salmoninae may be distinguished from the other salmonid fishes by the presence of a suprapreopercle bone, the absence of a dermosphenotic bone, and the broad separation of the parietals by the supraoccipital. Five genera may be recognized in the Salmoninae: *Brachymystax* Günther, *Hucho* Günther, *Salvelinus* Richardson, *Salmo* Linnaeus, and *Oncorhynchus* Suckley. A sixth genus, *Salmothymus* Berg (consisting of 2 species from Yugoslavia), is recognized by some authors (Berg, 1932, 1940) but it has been placed in the synonymy of *Salmo* by Regan (1920) and Nall (1930). I have examined a specimen of *S. ohridanus* and see no need for its separation from *Salmo*.

Brachymystax is characterized by the presence of fine teeth on the jaws (Pl. 13, D) (Tchernavin, 1923) and a small mouth; the jaw articulation is located below the eye rather than behind its rear margin as in the other 4 genera. The vomer is small with a short, toothless shaft. A single row of small teeth is continuous from the palatines across the head of the vomer to form an unbroken

oval series on the roof of the mouth (Fig. 1, B). There is a single species, *B. lenok*, which inhabits Siberia and eastern Asia.

Hucho is somewhat intermediate between *Brachymystax* and *Salmo*. As in *Brachymystax*, the shaft of the vomer is short and toothless, and the palatine and vomerine teeth form a continuous U-shaped series on the roof of the mouth (Fig. 1, C). As in *Salmo*, the jaws bear strong canine teeth (Pl. 13, H) and the jaw articulation is located well behind the eye. *Hucho* inhabits the Danube River, Siberia and eastern Asia (Dymond and Vladykov, 1934).

Salmo is characterized by well developed teeth on the shaft of the vomer so that the vomerine and the palatine teeth form a T on the roof of the mouth. There is a narrow toothless gap between the palatine teeth and those on the head of the vomer (Fig. 1, E). *Salmo* is further distinguished from *Salvelinus* because it has dark spots present on a lighter background. *Salmo* has a wide but discontinuous distribution, occurring in Europe, in eastern and in western North America, and in eastern Asia (Dymond and Vladykov, 1934).

Salvelinus has light spots present on a dark background and the shaft of the vomer is toothless (Morton and Miller, 1954: 122). There is a gap between the palatine teeth and those on the head of the vomer (Fig. 1, D), in contrast to *Brachymystax* and *Hucho*. *Salvelinus* is widely distributed across northern Europe, Asia, and North America and extends well into the temperate zones in these continents.

Oncorhynchus may be separated from the other genera because in the adult the dorsal fontanelles are grown over with cartilage (Tchernavin, 1938a) and the cartilaginous rostrum is azygous (Tchernavin, 1937: Fig. 2). As in *Salmo*, the shaft of the vomer is toothed, but there is a wide gap between the palatine and vomerine teeth (Fig. 1, F). *Oncorhynchus* is largely confined to the north Pacific Ocean and the area of Asia and North America bordering it; there is limited penetration of the Arctic Ocean from Bering Straits.

Fresh and preserved material of *Salmo* and *Salvelinus* was readily available for this study. As for *Oncorhynchus*, only the heads were available in the fresh state. The remainder of the data for *Oncorhynchus*, as well as for *Hucho* and *Brachymystax* was obtained from preserved specimens (Table II).

The Chondrocranium

THE OLFATORY REGION

The olfactory region of the salmonine chondrocranium is of the same general type as that described for the grayling and whitefishes, but some differences are apparent. A small but well-marked indentation or notch at the anterior end of the ethmoid cartilage (rostrum) of *Salmo gairdneri*, *S. trutta*, and *S. salar*, and the simple, bluntly pointed rostrum in the adult *Oncorhynchus*, are both unlike the modifications found in the grayling and whitefishes. The above difference between *Salmo* and *Oncorhynchus*, figured by Tchernavin (1937: 239; 1938a: 166; 1938b: 362), has been used as a basis for separating *Oncorhynchus* from *Salmo*,

in opposition to Regan's (1914: 407) belief that the salmon and trout should be united in the single genus *Salmo*. This anterior ethmoid notch is not well developed in *Salvelinus fontinalis* and it is even less noticeable in *Salvelinus namaycush* (Pl. 3, B), in which the ethmoid cartilage is rather broad and blunt as in *Thymallus* (Pl. 1, A and B). Observations made on preserved juveniles of *Oncorhynchus keta*, *O. nerka*, and *O. tshawytscha* (s. 1. 70 to 110 mm) indicate that the azygous condition illustrated by Tchernavin (1937, 1938a) is secondary, typical of salmon as they approach sexual maturity in the sea and after they return to freshwater. In the juveniles examined, the rostral cartilage appears bluntly truncate, much as in *Salvelinus namaycush*. The notch at the anterior end of the rostrum, so well developed in *Salmo gairdneri*, is very slight or absent. Thus, the condition observed in the juvenile *Oncorhynchus* appears to be intermediate between the forked rostrum of *Salmo gairdneri* and the simple blunt snout of the adult *Oncorhynchus*.

As in the grayling, the only constant ossification present in the ethmoid cartilage of the salmonines is the paired prefrontals (Pl. 3, B). The hypethmoid, a usual feature in the Coregoninae, is nearly always absent in the Salmoninae. Berg (1940: 425) noted its absence as a characteristic of the subfamily. Tchernavin (1938b: 356) stated that there is no true mesethmoid bone in *Salvelinus*. A small dorsal ossification was observed in 2 specimens of *Salvelinus fontinalis* used in this study. Tchernavin (1938b: 357) reported a similar ossification in 2 specimens of *Salmo trutta* from the Baltic Sea and in 2 specimens of *Salmo trutta caspius* (Kessler). Apparently a partially ossified ethmoid plate sporadically occurs through the subfamily but, due to the scanty study of chondrocranial material, it is only rarely observed or reported.

THE ORBITAL REGION

The most conspicuous feature of the orbital region of the salmonines is the large orbitosphenoid bone projecting ventrad into the interorbital septum. The orbitosphenoid has a large foramen in front, through which the olfactory tract passes before continuing anteriorly between the oblique eye muscles, through the cartilage mesial to the prefrontal, and thence to the nasal capsule. As in the grayling, the Y-shaped basisphenoid is also well developed in the salmonines and is supported by a partly ossified projection from the dorsal surface of the parasphenoid. The cartilaginous interorbital septum is better developed in the trout than in either the whitefishes or the grayling. It is particularly heavy in *Oncorhynchus*, but it is enlarged in old specimens of *Salvelinus namaycush*, *S. malma*, and *Hucho hucho*.

THE OTIC REGION

The Otic region of the chondrocranium is well ossified, especially ventrally and laterally. A large expanse of cartilage remains on the dorsal surface (Pl. 3, B). With few exceptions, this part of the chondrocranium is quite similar among all the salmonid fishes. One difference is the small cap-like opisthotic

covering the junction of the pterotic, epiotic, and exoccipital bones. The opisthotic is somewhat peculiar in *Oncorhynchus* because, ventrally, it has a splinter of bone which projects forward and touches the prootic. This was observed by Tchernavin (1938b: 362) and I found it in both *Oncorhynchus nerka* and *O. keta*, but not in *Salmo* or *Salvelinus*. The sphenotic is particularly well developed in the salmonines, forming a sturdy point of origin for the strong levator arcus muscle. The roof of the otic region is not so well ossified, much of the area being occupied by the dorsal fontanelles and a median (*taenia tecti medialis*, de Beer, 1937) and 2 lateral strips of cartilage (postorbital cartilage from auditory capsule, de Beer, 1937) (Pl. 3, B). Tchernavin (1923) noted that the salmonine supra-occipital does not have an anterior bony extension. However, some ossification continues forward on the cartilaginous bridge between the dorsal fontanelles in some specimens of *Salmo gairdneri*, *Salvelinus fontinalis*, and *S. namaycush*, as in *Thymallus* and *Coregonus*.

A pair of dorsal fontanelles is found in all genera of Salmoninae studied, at least in the young and juveniles, and they are proportionally smaller and more circular than in either the grayling or the whitefishes. Tchernavin (1937: 239; 1938b: 362) used the absence of dorsal fontanelles in *Oncorhynchus* as a character to separate *Oncorhynchus* from *Salmo*. Although the fontanelles are small and circular in *Oncorhynchus*, rather than large and oval as in *Salvelinus* and *Salmo*, they were observed in young specimens of *Oncorhynchus keta* (standard length 95 mm), *O. nerka* (83 and 103 mm), and *O. tshawytscha* (71 and 81 mm). In a hook-jawed adult male of the landlocked phase (kokanee) of *Oncorhynchus nerka* (252 mm), the dorsal fontanelles are present but much reduced in size. These observations were made on specimens which had not migrated to the sea. On larger specimens taken in the Pacific Ocean, cartilage had grown over and completely obliterated the dorsal fontanelles.

As in the graylings and whitefishes, the sagitta is the largest of the 3 otoliths found in the trouts and its position is identical. The otolith of the salmonines is relatively smaller and broader than in either the coregonines or the thymallines (Pl. 16). There appears to be some variation of the otolith among individuals, e.g. the sagitta of *Salmo gairneri* sketched for this study (Pl. 16, Q) looks much like the one figured for *Salmo trutta* by Frost (1925, Pl. XII). The otoliths of *Oncorhynchus keta* and *O. nerka* (Pl. 16, O and P) are more like the other salmonines than is the one of *O. quinnat* (*tshawytscha*) figured by Frost (1925). The salmonid otolith does not appear to have much generic significance.

Investing Bones

DORSAL ROOFING BONES

A good description and comparison of the skull bones of the Salmoninae is difficult and never completely satisfactory because of changes which occur at the time of breeding.

In his important contribution "Changes in the Salmon Skull" Tchernavin (1938a: 165) commented: "The skulls of adult migratory *Salmo* and *Oncorhynchus*

are subject to striking changes throughout the whole life of the fish. These changes are so marked that the study of the salmon skull becomes, in fact, a study of its changes. Many characters usually regarded as 'fortuitous variations' or as taxonomic distinctions are found to be features of particular phases of these regular changes." For this reason, special emphasis is here given to juvenile specimens in which modifications are less pronounced. This eliminates, to some extent, differences due primarily to the expansion of cartilage in the adult.

The supraethmoid, present in all salmonines, has the greatest taxonomic significance of all the dorsal roofing bones. It is fimbriate posteriorly with some of the finger-like projections overlapping the frontals. Laterally it borders the nasals but does not fuse or articulate with them. Anteriorly the supraethmoid is rounded or triangular, so that it fits between the backward extensions of the premaxilla without overlapping them. The salmonine supraethmoid is useful in classification because of its variation. One type is the widely divergent V-shaped form characteristic of *Oncorhynchus* (Pl. 12, F). In some large specimens, the posterior notch is so deep that the supraethmoid is almost bisected. Varying degrees of depth in the V-shaped indentation are noted in species of *Salmo*. In freshwater specimens of *Salmo gairdneri* (Pl. 12, K), for example, the supraethmoid is wing-shaped and similar to the grayling. *Salvelinus namaycush* and *Brachymystax lenok* lie at the other extreme. Their supraethmoid is long, narrow and irregular, and lacks the widely diverging arms (Pl. 12, I and J). *Salvelinus fontinalis* is similar to but not quite as extreme as the lake trout (Pl. 12, L). Kendall (1919: 80) used the proportional width-to-length measurement of the supraethmoid to separate *S. namaycush* from other chars. *Hucho* is similar to *Salvelinus* but in it the supraethmoid is short and broad (Pl. 12, H).

The frontal is a large, triangular bone covering most of the roof of the chondrocranium, as it does in the grayling and whitefishes. The most obvious difference is in the supraorbital canal, which is transmitted directly to the pterotic. In the trouts, unlike *Thymallus* and the coregonines, the dermosphenotic is absent. In adults of *Oncorhynchus*, the frontals are widely separated at the midline by the growth and expansion of cartilage. This extensive growth of cartilage in maturing *Oncorhynchus* even erodes away the bone so that the frontal is no longer very triangular and comes to a blunt point anteriorly. This divorce of the frontals is foreshadowed even in the young, in which the bones are partly separated by a strip of cartilage. The frontals of other species are more closely articulated at the midline and fusion across the frontals sometimes occurs in *Salvelinus fontinalis*.

The parietals in the salmonines are small rectangular bones that cover a small portion of the skull roof as compared to those of the grayling and whitefishes. They are completely separated by the supraoccipital and lie on the dorsolateral surfaces of the chondrocranium (Pl. 9, B).

In the trouts the extrascapulars are merely tubular bones, carrying the supratemporal canal, and are not expanded as in the whitefishes and grayling. There usually are 4 pairs but 5 or 6 sometimes occur and *Brachymystax* has only 3 pairs. The pair nearest the middle usually meet at the midline as in the

Coregoninae. This character is somewhat variable, however, as *Salvelinus fontinalis* and *S. namaycush* sometimes have a median extrascapular (Pl. 9, B) as is typical in the grayling.

The supraoccipital has become more important as a dorsal roofing bone in the Salmoninae. Not only the occipital crest but also a thin lamina of bone covering the exposed portion is of dermal origin (Pl. 3, B and 9, B).

As in other salmonids, paired nasals are located on either side of the supraethmoid. Paired pterotics, well developed but not particularly distinctive, also are present.

LATERAL SKULL BONES

The lateral surface of the head in the salmonines is less fully invested in bone than it is in either the coregonines or the thymallines. The bones either have been reduced or have not kept pace with the greater development of the musculature of the head.

Anteriorly the rounded premaxilla covers the dorsolateral surface of the skull. It is well toothed, bearing from 6 to 9 long, curved teeth. It does not quite touch the premaxilla from the opposite side. This separation may be greater in old adults, forming a ventral groove to receive the long, hooked mandible. Posteriorly the premaxilla articulates with the inwardly curved portion of the maxilla and is prevented from touching the palatine at this point. The ascending process of the premaxilla, which lies against the supraethmoid, is somewhat distinctive among the genera of salmonines. It is present in the young of all species, although it is not quite so well developed in *Oncorhynchus*. However, at maturity there are differences. In *Oncorhynchus*, the ascending process has become reduced and almost disappears, whereas in *Salvelinus* it is strong and extends well backward (Pl. 9, B). In *Salmo gairdneri*, *S. trutta*, *Hucho hucho*, and *Brachymystax lenok*, the ascending process is present (Pl. 13, C, H, and D), but it is not so pronounced as in *Salvelinus*.

The maxilla is a long, narrow, slightly curved bone which, except for size, is quite similar to that of the grayling. Teeth are well developed on the maxilla (except on anadromous species when in the sea) and extend along three-fourths the length of the bone (Pl. 10, C). In the migratory salmonines which spend part of their life in the sea, the teeth are short, curved and attached only to the skin. The anterior and posterior one-eighth of the maxilla is devoid of teeth. In juveniles (total length about 65 mm) teeth are fewer in number, but they are well developed in *Salvelinus namaycush* and are smaller and more numerous in *Oncorhynchus*, than in other species studied. In all salmonines, the maxillary teeth are always smaller than the premaxillary teeth (Pl. 13, C, D, and H).

The supramaxilla is a narrow splint-like bone slightly wider posteriorly and coming to a point anteriorly, similar to that in the grayling (Pl. 13, C, D, and H).

The circumorbitals usually number 7 bones (Pl. 10, C) though there are 8 in the grayling and whitefishes. The first 2 are the supraorbitals which do not bear a lateral-line canal.

The lachrymal, the 3rd bone in the circumorbital series, curves upward in front to meet the 2nd supraorbital. The infraorbital canal terminates in the lachrymal, which displays distinctive features. In *Salvelinus namaycush* and *Brachymystax lenok*, it is somewhat rounded in front, as in *Stenodus* but in *Oncorhynchus*, *Salmo gairdneri*, *S. trutta*, and *Hucho hucho* it is more rectangular, similar to that in *Thymallus*.

Behind the infraorbital, 3 (occasionally 4) postorbitals are found in the salmonines. The 2nd postorbital is the longest, whereas in the grayling and whitefishes (except *Stenodus*) it is the 1st postorbital that is the longest. A further distinction from the former 2 groups is noted in the direct articulation of the 3rd (uppermost) postorbital with the frontal and pterotic. The infra-orbital canal is transmitted directly to the lateral canal in the pterotic. No dermosphenotic is present in salmonines. Except in *Oncorhynchus*, the post-orbital bones fail by a wide space to reach the preopercle; often they extend less than half way across the cheek (Pl. 10, C). The 2nd postorbital of all adult Pacific salmon (*Oncorhynchus*) extends backward and touches the preopercle, as it does in *Thymallus*, *Coregonus* and *Prosopium* but not in *Stenodus*. This backward growth commences early and is already observed to be twice as broad as it is in lake trout specimens of 65 mm total length.

The dentary is a strong, well-toothed bone comprising the greater part of the lower jaw (Pl. 10, C). The number of teeth is variable but at least 10 are present, and in non-anadromous forms these are fused to the dentary. The teeth are fused also in juveniles of *Oncorhynchus* before they migrate to the sea. In specimens of *Oncorhynchus nerka* and *O. keta* obtained from the Pacific Ocean, the small teeth are loosely embedded in the skin. A similar condition exists in *Salmo salar* (Tchernavin, 1938a). As in the grayling, the lower arm of the dentary is the longer, but it does not extend far enough caudad to touch the retroarticular as it does in the coregonines.

As in other salmonids, the triangular-shaped angular bone fits into the curved mesial surface of the dentary. The inner surface of the angular has become ossified around the posterior end of Meckel's cartilage, which then extends forward to fit into the anteromesial groove in the dentary. The retroarticular is located at the posteroventral corner of the angular. Also present is a small coronomeckelian, located on the mesial surface of the angular and lying over Meckel's cartilage. Except for the contact of dentary and retroarticular in the Coregoninae, these 3 bones have little taxonomic significance among the salmonids.

The preopercle, in contrast with its prominently arched form in the grayling and whitefishes is only gently curved. The horizontal arm is only about one-fourth to one-third the length of the vertical arm (Pl. 10, C). It is attached by tough fascia to the corner of the lower jaw and quadrate. The preopercle is rather uniform among the Salmoninae. In the Salmonidae, the suprapreopercle is peculiar to the Salmoninae (Pl. 10, C). It is a small tubular bone lying between the dorsal tip of the preopercle and the pterotic. The 3 remaining opercular bones have little taxonomic significance at the generic level among the salmonids.

The branchiostegal rays in the Salmoninae are rather large fan-shaped bones covering much of the ventral surface of the head. They are generally more numerous in the salmon and trout than in the grayling and whitefishes. The minimum number 8, reported in *Salmo gairdneri* (Needham and Gard, 1959), is the same as that found in many species of *Coregonus* and *Prosopium*. The 11 branchiostegal rays found in *Salmo ohridanus*, *Salvelinus fontinalis*, and *Hucho perryi* is equal to the maximum for *Stenodus leucichthys*, but as many as 15 are present in *Salvelinus malma*. From 10 to 19 were counted by Clemens (1935: 105) in various species of *Oncorhynchus*. The number of branchiostegal rays is of limited taxonomic utility in the Salmoninae because of the variation and overlap among species. The posterior 2 or 3 rays are attached to the epihyal, the remainder to the ceratohyal.

VENTRAL BONES OF CRANIUM

The vomer has received considerable attention from ichthyologists because of its use as a systematic character to separate *Salmo* from *Salvelinus* and, further, to separate the lake trout from other chars. The vomer in the salmonines is much larger than in either of the other subfamilies. In *Oncorhynchus* and *Salmo*, it is a narrow flat plate armed with teeth along its entire length. The teeth are fused to the vomer in the juveniles but are small and deciduous when they migrate to the sea. In contrast, the vomer of the char (*Salvelinus*) is shaped like an inverted boat hull, with a dorsal keel and a ventral crest. Most of the teeth are borne on the anterior enlarged head, with few at most, on the crest. The tapering shaft is toothless. The toothed crest in the lake trout has been used to separate this species as a separate genus (*Cristivomer*), but Kendall (1914: 10; 1919: 70-80), Regan (1914: 408) and more recently Morton and Miller (1954) have shown that intermediate conditions exist in the Arctic chars. Nomura (1953: 263; 1954: 237) has used the presence and relationships of the teeth on the vomer and palatines as a means of separating 3 genera of salmonids (*Oncorhynchus*, *Salmo*, and *Salvelinus*). In *Oncorhynchus*, the teeth on the roof of the mouth are arranged in 2 lateral bands on the palatine bones, a toothless gap, and a straight band on the shaft of the vomer (Fig. 1, F). In *Salmo*, the shaft of the vomer is toothed and there is little or no gap between the palatine and vomerine teeth (Fig. 1, E). The toothed outline thus formed is T-shaped. In *Salvelinus*, teeth are present on the palatines but with a short gap between them (Fig. 1, D). *Brachymystax* and *Hucho* are alike in that the shaft of the vomer is toothless and the palatine teeth are continuous with those on the vomer, thus forming a semicircular band of teeth around the anterior margin of the palate (Fig. 1, B and C).

The digitate anterior part of the parasphenoid is overlapped by the vomer in all species of Salmoninae studied. The anterior end of the parasphenoid is rather flat, but when it reaches the otic region, it bends upward to form the floor and most of the sidewalls of the posterior myodome.

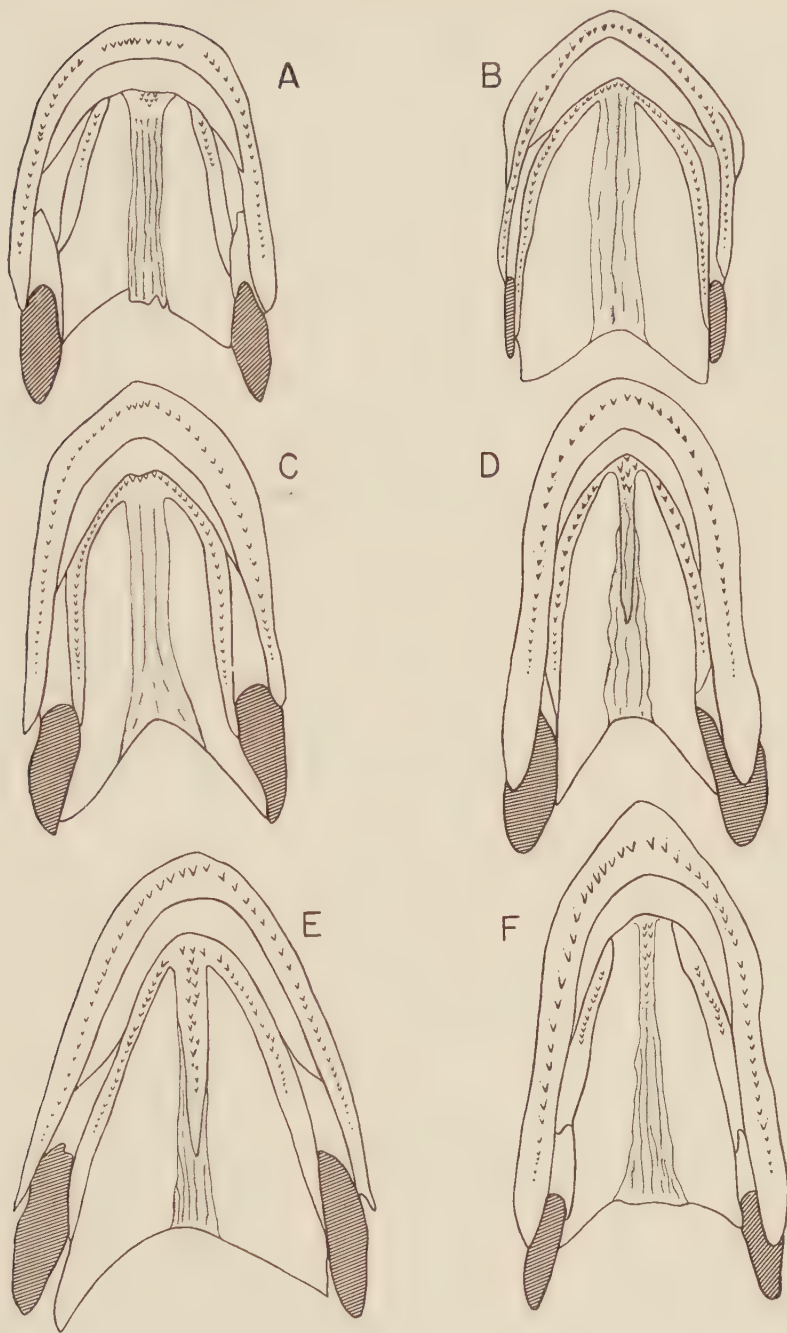


FIG. 1. Palatine and vomerine teeth of Salmonidae.

- A. *Thymallus arcticus*, UMMZ 172465, about 0.9×
- B. *Brachymystax lenok*, UMMZ 172490, about 1.7×
- C. *Hucho perryi*, UMMZ 172493, about 1.7×
- D. *Salvelinus fontinalis*, UMMZ 172462, about 0.7×
- E. *Salmo trutta*, UMMZ 172470, about 0.65×
- F. *Oncorhynchus nerka*, UMMZ 167467, about 0.7×

Visceral Arches

PALATOQUADRATE ARCH

The palatine is well toothed in all the salmonines, although the teeth are small and free from the bone in species of *Oncorhynchus* and *Salmo* when they enter the sea. In all genera except *Oncorhynchus* the palatine teeth are more or less continuous with those on the vomer (Fig. 1). Anteriorly the palatine is larger and bears two well-developed cartilaginous knobs. The first articulates with the ethmoid cartilage in front and the second behind the prefrontal bone. Posteriorly the palatine narrows to a thin splint and is overlapped by the ectopterygoid.

The distinctive difference in the salmonine quadrate lies in its position rather than in its size or shape. In the graylings and whitefishes, its articulation with the angular is below the eye, whereas in trouts (except *Brachymystax*) it lies well back of the orbit (Pl. 10, C). In *Brachymystax* the quadrate articulation is located in a line with the posterior border of the eye. Its relationship to the ectopterygoid, mesopterygoid, symplectic, preopercle and palatoquadrate cartilage is similar.

HYOID ARCH

The hyomandibulars, symplectics, interhyals, epihyals, ceratohyals, and hypohyals in the Salmoninae differ little from those of the grayling and whitefishes.

The basihyal is cartilaginous, overlaid with a rather long, well-ossified lingual plate (Pl. 6, B). The lingual plate of the salmonines bears from 8 to 12 strong teeth arranged in a series around the outer 3 edges of the bone, although in *Hucho perryi* a few small teeth were observed in the centre of the bone as well. The posterior edge of the lingual plate overlaps the first basibranchial. The well-toothed condition is reminiscent of *Coregonus artedii*, *Prosopium coulteri*, and *Stenodus leucichthys*, but the dental arrangement is different in that teeth are scattered over the bone in the three species of whitefishes. The elongate shape is somewhat like that in *Stenodus* and *C. artedii*, but it is not at all like the spatulate lingual plate in *Thymallus arcticus* (Pl. 6).

BRANCHIAL ARCHES

The basic pattern of the branchial skeleton is similar throughout the salmonid fishes. All, including the trouts, have 3 pairs of ossified pharyngobranchials, the first pair being attached to the parasphenoid. A small pharyngeal plate is found on the 3rd pharyngobranchial (Pl. 6, B). The plate is small and poorly developed with only 1, 2, or 3 teeth present in *Salmo salar*, *S. trutta*, and *Brachymystax lenok*; it is like *Prosopium cylindraceum*, *Coregonus artedii*, and *C. clupeaformis*. The pharyngeal plate is better developed in the other salmonines studied, especially *Salvelinus fontinalis*, *S. namaycush*, *Hucho hucho*, and *H. perryi*. The last 4 species are comparable to *Thymallus arcticus* but the teeth are not as numerous as in *Stenodus leucichthys*.

There are 4 pairs of epibranchials, the 4th being atypical and bearing a pharyngeal plate as in the grayling and whitefishes (Pl. 6, B). Five pairs of ceratobranchials are present, the 5th being broad, anteriorly, and covered with the 3rd and largest pharyngeal plate (Pl. 6, B). Three pairs of hypobranchials are present and are similar in shape and mode of articulation to the same bones in the grayling. Short blunt gill rakers are present on the anterior faces of all 5 arches. When present on the posterior surfaces of the arches, the gill rakers are much smaller and are irregular in occurrence. Tchernavin (1938a) mentioned their presence on *Salmo salar* but said they were lacking in *Oncorhynchus*. The presence of posterior gill rakers was verified on some specimens of *Oncorhynchus nerka*, *Salmo gairdneri*, *S. clarki*, *S. ohridanus*, *Salvelinus fontinalis*, *S. namaycush*, *Hucho hucho*, *H. perryi*, and *Brachymystax lenok*.

There is a series of 4 basibranchial bones which lie on the floor of the pharynx. In all salmonines 1 or 2 dermal basibranchial plates cover the area between the middle of the 2nd basibranchial and the middle of the 4th basibranchial (Pl. 6, B). They are fused to the 3rd basibranchial and may or may not bear teeth. The teeth are well developed in *Hucho perryi*, *Salmo clarki*, and *Salvelinus namaycush*, and are reported to be present in most other species of *Salvelinus*. In *Salvelinus fontinalis* the teeth are feebly present or are absent (Pl. 6, B), but they are lacking in all other salmonine species studied (including *Salmo gairdneri*, *S. salar*, *S. ohridanus*, *Hucho hucho*, *Oncorhynchus tshawytscha*, *O. nerka*, and *Brachymystax lenok*). The basibranchial plate corresponds to that found in the genus *Prosopium*. The dentigerous condition, when present, is not like that found in *Coregonus artedii* and *Stenodus leucichthys*, in which the teeth are implanted in skin.

UROHYAL

A urohyal is present in all trouts, its shape being similar to that in the related forms studied.

Axial Skeleton

VERTEBRAL COLUMN

The number of vertebrae in the salmonines ranges from 55 in *Salmo trutta* (Tåning, 1952), *S. gairdneri* (Needham and Gard, 1959), and *Salvelinus fontinalis*, to 72 in *Oncorhynchus tshawytscha* (Foerster and Pritchard, 1935). Tåning (1952: 184) has cited counts of 53 and 54 in *Salmo trutta* but he suggested the possibility that they stem from vertebral fusions. The maximum number of vertebrae (72) is higher than in any other salmonid.

The shape and size range of the vertebrae are the same as in the grayling. Neural arches and spines are borne on the centra. The arches lie in circular pits, and those anterior of the dorsal fin are not fused to the centra. The neural spines anteriorly of the dorsal fin are bifurcated, while those behind it are simple and slope caudally. The last three or four are somewhat expanded. Epineurals are present on the first 30 to 36 vertebrae and slant caudally from near the base of the neural arches.

Ventrally the centra bear rounded pits which receive the parapophyses supporting the ribs. The parapophyses of about the first 30 vertebrae are not fused to the centra. Posteriorly, they lie progressively farther forward on the centra and are fused with them. The parapophyses bear short pre- and postzygapophyses that do not articulate between centra. Long, 2-headed pleural ribs articulate with the parapophyses. The last 6 or 8 ribs have rounded heads and are loosely attached to the longer parapophyses. Epipleurals are typically lacking among the salmonines. Among the species studied, they were found only in *Salvelinus fontinalis*, and in this species they are subject to individual variation, being developed in only 5 of 14 specimens examined. In these 5 the ribs were considerably expanded dorsally, the expanded part forming a free spine that is dichotomous on many ribs. From 15 to 23 pairs of ribs bear epipleurals.

The parapophyses of the 5 to 7 precaudal vertebrae are elongate and bridged, forming haemal arches and a haemal canal. The caudal vertebrae are characterized by the presence of caudally-directed haemal spines; the last 3 or 4 (excluding the 7 hypurals) of which are somewhat expanded. The number of caudal vertebrae is positively correlated with the total number of vertebrae present. Thus, in a specimen of *Salvelinus fontinalis* having 56 vertebrae, 22 are caudal, while in *Oncorhynchus tshawytscha* with 69 vertebrae, 30 may be caudal vertebrae.

The basic structure of the caudal fin is fairly constant among the salmonines. There is little variation in the number of principal caudal rays, which typically number 19, occasionally 18 or 20. Three upturned terminal vertebrae, 7 hypurals, and 3 pairs of uroneurals are present as in the grayling and whitefishes. The dorsal crest of the anterior uroneural is more strongly developed in *Salvelinus fontinalis*, *Salmo gairdneri*, and *Hucho perryi* (Pl. 14, A and C, Pl. 15, C) than in *Oncorhynchus*. Two epurals usually are present in *Salvelinus fontinalis*, *S. namaycush*, *Salmo salar*, *S. trutta* (Pl. 14, A, B, E, and F), and occasionally in *Oncorhynchus keta*, *O. nerka*, and *O. tshawytscha*. This seems to be a variable character, however, because sometimes both the arch and the spine belonging to the 3rd terminal centrum may be present, the spine alone may be absent, or both may be absent. *Salmo gairdneri* regularly has 3 epurals (Pl. 14, C). Three epurals occasionally are present in *Salmo trutta*, (Pl. 14, D), *Oncorhynchus nerka*, *O. tshawytscha*, *O. kisutch*, and *Hucho perryi* (Pl. 15, A and C). Apparently in these species either the 3rd terminal neural arch has been lost or it has become fused with the anterior uroneural, with the neural spine remaining as an epural. A cartilaginous urostyle curves dorsally and terminates in a blunt tip between the roots of the caudal fin rays.

MEDIAN FINS

The dorsal fin of the trouts is similar to that of the grayling, except that it has fewer rays. None of the Salmonines counted had more than 16 dorsal rays, which is one less than the minimum recorded for a grayling. The dorsal ray count in the trouts is of little value as a taxonomic character, because it may vary from a low of 11 in *Salvelinus fontinalis* to a high of 16 in *Oncorhynchus tshawytscha*.

The variability in each species is about 4 rays; for example, the range for *Salvelinus fontinalis* is 11 to 14. The number of rays corresponds closely with that in the coregonines. As in the grayling and whitefishes, the dorsal rays are supported by a series of 3 pterygiophores. Fourteen to 20 interneurals lie between the atlas and the dorsal fin and project ventrad between the bifid neural spines.

Except for location, the characteristics of the anal fin are the same as the dorsal fin. Although it does not appear to be a particularly significant character, the higher number of anal rays (16 to 20 recorded for the Pacific salmon) has been used as one means of separating the genus *Oncorhynchus* from the rest of the trouts. This figure is higher than those recorded by Foerster and Pritchard (1935: 110) who did not count those rays which are less than one-half as long as the longest ray. However, it is impossible to separate *Salmo* from *Oncorhynchus* on this basis alone as the numbers overlap to some extent, and vary from 11 to 15 anal rays (the latter observed in one specimen of *Salmo gairdneri*). Although no overlap occurs between the North American species of *Oncorhynchus* and *Salmo*, an intermediate condition exists in the Asiatic *Oncorhynchus masou*, which has from 13 to 15 anal rays. The same observation was made by Regan (1914: 407). With the exception of *Oncorhynchus*, the number of anal rays in the salmonines overlaps both the thymallines and coregonines. The long antero-dorsally directed pterygiophores are equal to, or 1 or 2 less than, the number of anal rays present.

Appendicular Skeleton

PECTORAL GIRDLE

There is little to add in a description of the pectoral girdle of the salmonines that has not already been mentioned for the coregonines and thymallines. The same bones are present, and in the same locations. The scapular foramen is entirely within the scapula. A mesacoracoid, and three postcleithra are present, with the 3rd being long and pointed, as in *Thymallus* and *Coregonus*. The 1st postcleithrum usually overlaps the 2nd and if not, there is only a short gap between them. Four actinosts are commonly present, occasionally 5, and 6 were found in a specimen of *Salmo gairdneri* (Norden, 1959).

The number of rays in the pectoral fin varies from 12 in *Salmo trutta* and *Salvelinus fontinalis* to 17 in *Oncorhynchus nerka* and *O. keta*. In general, the fin-ray count for *Oncorhynchus* is slightly higher than for trouts, with a range of 14 to 17 rays.

PELVIC GIRDLE

The pelvic girdle of the trouts is not different from other salmonid fishes, consisting of a pair of L-shaped basipterygia which meet at two points in the midline. A curved pterygiophore, an axillary process, and 8 to 11 fin rays are present. A minimum of 8 pelvic rays is recorded for *Salvelinus fontinalis*, and a maximum of 11 in *Salmo gairdneri*, *Oncorhynchus nerka*, and *O. tshawytscha*.

THE CAUDAL SKELETON

The 3 upturned vertebrae in the caudal fin provide a major characteristic of the Salmonidae. There is no basic morphologic difference in the caudal skeleton among the Salmoninae, Coregoninae, and Thymallinae (Gosline, 1960). The 7 hypurals, 3 pairs of uroneurals and cartilaginous urostyle are common to the 3 groups. The greatest variation is noted in the anterior (largest) pair of uroneurals and the epurals. The Coregoninae and Thymallinae are relatively stable in these 2 characteristics, both subfamilies have 2 epurals and the dorsal arm of the first uroneural is only slightly enlarged (Pl. 14, G and H, Pl. 15, B). The Salmoninae are more variable, and may have 2 or 3 epurals and an enlarged dorsal crest on the first uroneural (Pl. 14, Pl. 15, A and C).

From study of developmental stages at the onset of ossification to adulthood, it appears that paired uroneurals 2 and 3 are remnants of the neural arches which belong to the urostyle, whereas the 1st pair of uroneurals is developed from neural arches derived from the last 2 or 3 upturned vertebrae. The epurals represent the neural spines belonging to these arches. It appears further that there is progressive reduction in parts and a change in their relation to the centra. Thus, if the primitive condition consists of 3 distinct neural arches with spines, the following variations have occurred. (1) The last 2 neural arches have fused to form the 1st pair of uroneurals and the neural spines have remained separate as 2 epurals. A 3rd neural arch and spine remain but they are separate from the 3rd terminal centrum (Pl. 14, A). Specimens of this type have been found in *Salvelinus fontinalis*, *S. namaycush*, and *Salmo trutta*. (2) The preceding situation maintains, but the neural spine from the 3rd terminal vertebra is lost and the arch remains separate (Pl. 14, B). This type was noted in specimens of *Salvelinus fontinalis* and *S. namaycush*. Specimens falling into these 2 categories each have 2 epurals. (3) The first pair of uroneurals may be derived from the last 3 neural arches, but the 3 spines remain and have become separated from it as epurals (Pl. 14, C and D). Individuals of this type have been found in *Oncorhynchus gorbusha*, *O. kisutch*, *O. nerka*, *O. tshawytscha*, *Salmo gairdneri*, and *S. trutta*. Vladykov (1954: 914) mentioned the 3 epurals that are present in *Salmo gairdneri* and the whitefishes. In this type, the arch and spine belonging to the 4th terminal centrum is complete but free from it. (4) The first uroneural is derived from the last 3 neural arches, but a spine has been lost and there are only 2 epurals. However, the fourth terminal arch and spine are complete, but separate from the centrum (Pl. 14, E and F). Individuals of this type were found in *Oncorhynchus keta*, *O. nerka*, *O. tshawytscha*, *Salvelinus namaycush*, *Salmo salar*, and *S. trutta*. (5) In some species, the spine of the 4th vertebra is separated from its arch and is located farther backward, forming what appears to be a 3rd epural. However, it obviously belongs to the 4th vertebra. Therefore, the derivation of the 1st uroneurals and the 2 epurals is believed to be the same as in type 4 (Pl. 14, G and H; Pl. 15, B). This has been observed in specimens of *Coregonus artedii*, *C. clupeaformis*, *Prosopium coulteri*, *P. cylindraceum*, *Stenodus leucichthys*, and *Thymallus arcticus* (possibly *Oncorhynchus tshawytscha*) (Pl. 15, A).

(6) The spine belonging to the 4th terminal vertebra has either disappeared or has moved backward and lies so close to the 2 epurals that it cannot be distinguished from them. The 1st uroneural is derived from the last 3 arches, 3 epurals are present, and in some cases the arch belonging to the 4th terminal centrum is in the process of disappearing (Pl. 15, A and C). This type was observed in *Oncorhynchus tshawytscha*, *Hucho perryi*, and *Brachymystax lenok*.

It can be readily seen that considerable variation exists in the caudal supporting skeleton of the salmonid fishes. In the thymallines and coregonines the size and shape of the 1st uroneural, its relation to the epurals, and the modification of the 4th terminal neural arch and spine appear fairly constant, and these structures are quite similar. It is in the salmonines that most variations occur. Thus, in this particular character, the graylings appear to be closer to the whitefishes. However, too much significance should not be attached to the instability of the caudal skeleton in the trouts.

EXTERNAL ANATOMY

Externally the graylings, trouts and whitefishes have much in common which emphasizes their close mutual affinities. All are soft-rayed fishes, having small to moderate-sized cycloid scales, an adipose fin, scaleless head, abdominal pelvic fins, and an axillary process or scute at the axil of the pelvic fin. Although these characters are not unique to this group, taken in combination they are useful in separating salmonids from other groups of fishes.

The graylings, trout, and whitefishes have certain distinguishing features which make it possible to separate the 3 groups. The enlarged dorsal fin, with 17 to 24 rays, sets the graylings apart from the coregonines and salmonines. The smaller scales (usually more than 100 along the lateral line) and the large, well-toothed jaws are distinctive characters of the trouts. The usually silvery colour, small, weak teeth, and usually larger scales characterize the whitefishes.

External characters possessed in common by the graylings and trouts are the toothed maxilla and the similar colour pattern of a bluish- or greenish-gray background mottled with circular spots, regularly found on most adult trout and grayling.

Distinctive features shared by graylings and whitefishes include the relatively deeply forked caudal fin, small mouth, and large scales. The scales in the lateral line of the graylings vary from 72 to 110 (Svetovidov, 1936). For the whitefishes the range is from 54 (*Coregonus tugun*, Berg, 1948 and *Prosopium coulteri*, Eschmeyer and Bailey, 1955) to 120 (*Stenodus leucichthys*, Berg, 1948).

A study of the scales of *Thymallus arcticus* reveals a closer alliance with the coregonines than with the trouts. This is contrary to the view held by Kendall (1935: 8) that the scales of *Thymallus* are more trout-like. Although Lagler (1947) pointed out that scales are of only limited use as taxonomic characters, the salmonid scale may in general be considered archaic. Lagler regarded closely set, regular circuli and the lack of radii as primitive. Measured by these criteria the trouts are most primitive, and *Stenodus* has the most highly specialized scales,

with secondary radii best developed on the posterior (exposed) field. The condition in *Stenodus* is approached by those in *Coregonus clupeaformis*, *C. artedii*, and *Prosopium cylindraceum*. Occasionally a few short secondary radii are present on the posterior field in *Thymallus arcticus*. The shape of the grayling scale is distinctive, especially the embedded portion, which has a wavy margin with 4 to 6 indentations. The closest approach to this condition is found in the coregonines, which have 2 indentations. The embedded field of the trout scale is round.

Sexual dimorphism is present to some extent in all salmonids. It is least well developed in the coregonines, which have pearl organs. These are said by Koelz (1929: 318) to be present on the head and sides of the body in both sexes in *Coregonus clupeaformis*. In *Prosopium cylindraceum*, according to Koelz, they are developed in both males and females but only on the body. In the Great Lakes ciscoes, pearl organs are well developed only in males and are of uniform thickness over the head and sides of the body. Pearl organs have also been observed on the male *Salvelinus namaycush* (Vladykov, 1954.) The enlarged hook on the lower jaw of male salmonines is a sex-influenced character. In the grayling, the dorsal fin rays of the male elongate so that they extend up to or slightly beyond the adipose fin. In the female, the dorsal rays (when depressed) fail to reach the adipose fin.

MUSCULATURE

A comparative study of the muscles was made on 3 species, *Thymallus arcticus*, *Coregonus artedii*, and *Salvelinus namaycush*, representing the 3 sub-families. Papers on the musculature of the chinook or king salmon, *Oncorhynchus tshawytscha* (Greene and Greene, 1913) and the Atlantic salmon, *Salmo salar* (Tchernavin, 1953), were followed and the muscles described were found in the 3 species. No significant differences in musculature were observed; that is, no loss or change in position of a muscle was noted. This is not unexpected since few bones are absent from any of the species. Those that are absent (i.e., orbitosphenoid, hypethmoid, suprapreopercle, dermosphenotic) are not important to the origin or insertion of muscles. The greatest variation observed was in size, particularly of the jaw muscles. This relates to feeding habits for most of the salmonines, with large mouths and strong jaws, are piscivorous. Thus, the *adductor mandibularis* is large in *Salvelinus namaycush*, intermediate in size in *Thymallus arcticus*, and small in *Coregonus artedii*. Bones which provide attachment for muscles are influenced by their size. For example, the sphenotic bone in *S. namaycush* is large and projects laterally, affording origin for the well-developed *levator arcus palatini* muscle, which elevates the palate. The hyomandibular is also massive in the adult lake trout in which it forms part of the origin of the *adductor mandibularis* muscle and the insertion of the *levator* and *adductor arcus palatini* muscles. The latter muscles originate in part on the orbitosphenoid, pterosphenoid, sphenotic, and pterotic bones in *Salvelinus*, but in *Thymallus*, which does not have an orbitosphenoid, the origin is on the pterosphenoid.

INTERNAL ORGANS

The visceral organs are structurally similar among all the salmonid fishes studied. The gullet bears longitudinal ridges on its inner surface, which continue into the U-shaped stomach. In specimens gorged with food the ridges disappear. A U-shaped stomach appears to be characteristic of the salmonid fishes.

In the grayling, the spleen is usually elongate and attached to the apex of the stomach by peritoneum. In the salmonines, the spleen is more or less triangular or heart-shaped. Little significance can be attached to this difference because much variation exists between the ribbon-shaped spleen of the adult grayling, the small triangular organ in the brook trout, and the intermediate conditions common in the coregonines. The stomach is separated from the intestine by a pyloric sphincter. The anterior end of the intestine is beset with numerous blind tubes, pyloric caeca, which are present in all salmonid fishes. The number of pyloric caeca varies widely, from 11 to over 200. Great diversity in number is noted in forms which are obviously very closely related, a fact which supports the interpretation of Morton and Miller (1954: 122) that the character should be accorded only specific significance in this group. The pyloric caeca of 8 adult grayling from Montana yielded the following counts: 17 (1), 18 (1), 19 (1), 20 (2), 21 (1), 22 (2). These counts are close to those recorded by Eschmeyer and Bailey (1955: 172) for *Prosopium coulteri*, which has a range of 15 to 23 caeca. Svetovidov (1936) reported from 11 to 25 caeca in the Eurasian graylings. Among salmonines, DeLacy and Morton (1943: 90) cited a low of 21 in *Salvelinus malma*, and Vladykov (1954: 913) gave 20 as the lowest count in *Salvelinus alpinus*. The lower part of the intestine is encircled with annuli which become more conspicuous near the anus. This increased absorptive area is equally well developed in all three groups. A bilobed liver and gall bladder also are present. The bile duct enters the duodenal part of the intestine a short distance below the stomach. The large, single-lobed swim bladder connects to the gullet just above its entrance to the stomach.

A pair of pseudobranchs are present in all salmonid fishes. They consist of a few gill filaments lying over the anterior edge of the hyomandibular and the dorsal margin of the metapterygoid bones.

REPRODUCTION AND LARVAL STAGES

The reproductive organs of the three subfamilies are similar, with no differences in shape or location of the gonads. The testis is a long (well over half the length of the intestine), rather flat organ commencing at the anterior end of the stomach and extending much of the length of the peritoneal cavity. The sperm duct, located on the mesial surface of the testis, continues beyond the posterior tip of the testis to the urogenital opening. The pair of sperm ducts join near their external aperture.

The ovaries are of much the same shape as the testis in immature specimens, but in mature spawning females they become turgid with eggs and fill much of the

body cavity. The eggs do not normally break out into the abdominal cavity but are contained in oviducal folds of peritoneum which become narrow and tubular posteriorly just before they pass to the exterior.

The chief apparent difference in the eggs of the trouts, whitefishes, and graylings is in size. The average diameter of the unfertilized grayling egg is about 2.5 mm. This is about the size of the egg reported for the coregonines. That of *Coregonus clupeaformis* was given as 3.0 mm by Price (1934: 290), and Fish (1932: 308, 311) reported the average egg diameter of *Coregonus artedii* to be 2.25 mm and of *C. clupeaformis* 2.8 to 3.0 mm. Smith (1956: 125) gave 1.88 mm as the average diameter of *C. artedii* eggs at the time of spawning in Green Bay. Sigler (1951: 14) gave the egg size of *Prosopium williamsoni* as varying between 1.94 and 2.12 mm and Brown (1952: 110) gave 3.7 as the average diameter of water-hardened eggs for that species. The eggs of the salmonines are somewhat larger. Brown and Kamp (1942: 199) gave the average measurement for *Salmo trutta* as 4.94 mm. Vladykov (1954: 906) recorded the average diameters of eyed eggs from *Salvelinus fontinalis* as 4.0 to 4.4 mm, *S. namaycush* as 5.7 to 5.8 mm and *Salmo salar* as 5.4 to 6.8 mm. Tchernavin (1923) described the spawn of *Brachymystax* as fine, but gave no measurements. In general, the salmonine egg is about twice the diameter of the whitefish and grayling egg. This presumably accounts for the absence of a postlarval stage in the salmonines, whereas such a stage is present in the coregonines and thymallines.

Winn and Miller (1954: 276) defined postlarval life as "the period after the adsorption of the yolk to a stage when the fish resembles the juvenile." In the grayling, the transformation from postlarva to juvenile may be recognized by the loss of the continuous fin fold, the development of parr marks and commencement of ossification in the fin rays. This occurs when the young fish have reached a total length of 33 to 40 mm about 64 to 78 days after hatching. At a total length of 15.5 mm and an age of 16 days after hatching, the grayling is in the postlarval stage and the yolk is completely absorbed. At the same length, the lake trout, on the other hand, has a large yolk sac (measuring 7.25 mm in length and 4.5 mm in width). Day-old grayling (total length about 11.0 mm) have a small yolk sac (3.2 by 2.0 mm). Watling and Brown (1955: 93) recorded an average size range of 2.5 to 2.8 mm in the length of the yolk sac on the day of hatching. The yolk sac disappears about 13 days after hatching. Early stages for *Coregonus artedii* and *C. clupeaformis* have been described and figured by Fish (1932: 308-315) which are similar to those of *Thymallus arcticus* of the same age. When young lake trout are about 30 mm in total length the continuous fin fold has disappeared and parr marks have appeared; they then look like juveniles. In grayling of comparable length, the continuous fin fold has disappeared but the adipose fin is long and parr marks have not yet appeared. The grayling, now 52 to 55 days old, are still in the postlarval stage. Seventy-eight days after hatching, the grayling have reached a total length of 40 to 50 mm and are now developed juveniles with parr marks, a long dorsal fin and considerable ossification in the fin rays, vertebrae and some of the skull bones. Lake trout of similar size are in the same stage of ossification.

Parr marks, consisting of black pigment under the skin in a pattern of vertical bars or oval blotches along the side, are a rather common feature among the salmonids. The grayling has an average of 13.4 oval parr marks which are bisected by the lateral line. Parr marks also are present, at least in the young, in the genera *Salmo*, *Salvelinus*, *Brachymystax*, *Hucho*, *Oncorhynchus* (except *O. gorbuscha*, Foerster and Pritchard, 1935) and *Prosopium*. Young of *Prosopium abyssicola* and *P. gemmiferum* were not available for this study. They are absent from *Stenodus* and *Coregonus*.

The development of the young grayling has much in common with that of both the coregonines and the salmonines. The size of the egg and the postlarval stage suggest a closer relationship with the whitefishes, but the possession of parr marks tends to link *Thymallus* with the trouts and *Prosopium*. In the latter character, it is *Stenodus* and *Coregonus* that are set apart, and Walters (1955: 289) used this as one reason for segregating *Prosopium* as a genus distinct from *Coregonus*.

FOSSIL SALMONIDAE

The origin of the suborder Salmonoidei has been variously placed between the Upper Cretaceous and the Lower Eocene. Cockerell (1919) and David (1946a) have described fish scales from the Upper Cretaceous as belonging to or closely related to the family Salmonidae. Cockerell (1919) stated that the scales bear a resemblance to the Thymallidae, but since scales are of questionable taxonomic value, it is well not to attach too much significance to them. A fossil salmonid fish *Thaumaturus furcatus* (Reuss) has been reviewed by Laube (1900) from the Miocene of Bohemia. From the description and figure of the single caudal vertebra, it seems likely that this fish is allied to the Argentinidae or Osmeridae, although Berg (1940) erected a new family, Thaumaturidae, for this genus. Laube (1901) described as thymallids two fossil species, *Protothymallus lusatus* and *P. princeps*, from the Miocene of Bohemia. The figures give no basis for believing that they are more closely related to *Thymallus* than to any other salmonid. They do, however, show 3 upturned caudal vertebrae.

The few papers published on fossil salmonoids indicate that the Argentinidae and Osmeridae were separated from the Salmonidae at the beginning of the Miocene. Eastman (1917) reported an undetermined fossil related to *Osmerus* from the Oligocene or Lower Miocene of Montana, David (1943) described a form belonging to the family Bathylagidae from the Upper Miocene of California, and Weiler (1943) described 3 species of *Argentina* from fossil otoliths found in the Upper Tertiary of Romania.

Fossil remains of the salmonids are scanty and, partly for this reason, the recent genera and species are believed to be of rather modern origin, perhaps Pliocene or early Pleistocene. One reason for the scarcity of fossil material is the lack of interest by paleontologists in the ichthyofauna of these last two epochs. Perhaps the best known salmonid fossil is of *Rhabdofario*, described by Cope (1870) from the Pleistocene of Idaho and believed by Cope to be closely allied to

Salmo. Another possible explanation for the paucity of fossil salmonids rests on an ecological preference for habitats that are not conducive to easy fossilization.

Just where the separation of the coregonines, thymallines, and salmonines occurred poses a problem. The only available fossil material is from 2 or 3 scales obtained from the Upper Eocene or early Oligocene of California, which David (1946a) used to describe two new fossil species assigned to the Coregonidae. One of the scales shows similarity with the scales of *Stenodus*, the other, with those of *Coregonus nigripinnis*. As previously mentioned, little reliance should be placed on these two species. Good fossil material of the Salmonidae is a prime desideratum in a solution of the evolutionary history of the group.

SYSTEMATIC POSITION OF THE SALMONIDAE

Seven families (Salmonidae, Plecoglossidae, Osmeridae, Argentinidae, Salangidae, Retropinnatidae, and Aplochitonidae) at present are assigned to the suborder Salmonoidei. The osteology and relationships of the Osmeridae, Argentinidae, and Plecoglossidae have been worked out by Chapman (1941a, 1941b, 1942), and I have had study material available for these families (Table III). The Salangidae, Retropinnatidae, and Aplochitonidae were not studied.

In the Argentinidae, such characters as the placement of the paired fins, presence of an adipose fin, orbitosphenoid, basisphenoid, mesocoracoids, 3 postcleithra, epipleural spines, opisthotics, an open posterior myodome, toothed palatine and vomer, toothless maxilla, and the parietals meeting in the midline are found to be common also to some or all representatives of the Salmonidae. The Argentinidae are distinguished from the Salmonidae by the presence of one or two (Gosline, 1960) upturned caudal vertebra, the first uroneural does not extend forward beyond the penultimate centra (Gosline, 1960), edentulous premaxillae, lack of supramaxillae, the strong attachment of the palatine to the ethmoid region, and a swim bladder that lacks a connection with the gut (Cohen, 1958).

Features common to some species of both the Osmeridae and the Salmonidae are the presence of opisthotics, mesocoracoids, epipleurals, a toothed basibranchial plate, a shaftless but toothed vomer, an adipose fin, parietals which may or may not be separated by the supraoccipital, and an open posterior myodome. The Osmeridae are distinct from the Salmonidae because they have toothed mesopterygoids, a single upturned caudal vertebra, proethmoids, and a pouch-like stomach, which in *Osmerus mordax* has from 4 to 6 pyloric caeca.

The Plecoglossidae bear numerous resemblances to at least some of the Salmonidae in that they lack an orbitosphenoid and a basisphenoid, have numerous pyloric caeca, a toothed basibranchial plate, mesocoracoid bones, an adipose fin, and pseudobranchia. The Plecoglossidae are distinct in that they have no postcleithra, no supramaxillae, a single upturned caudal vertebra, toothed mesopterygoid, toothless vomer, and specialized oral organs.

These 3 families are of interest in this study because of the loss or modification of certain characters which appear to be distributed somewhat haphazardly

among the salmonids. For example, the orbitosphenoid is absent in the graylings, osmerids, and *Plecoglossus*, but is present in the trouts, whitefishes, and argentines. The basibranchial plate is present in the osmerids, trouts, *Plecoglossus*, and *Prosopium* but is absent in the argentines, graylings, *Coregonus*, and *Stenodus*. In the family Osmeridae, 3 genera have the parietals meeting in the midline, whereas 3 others have the parietals separated by the supraoccipital, thus paralleling the condition in the Salmonidae. Thus certain characters which seem, at first, to be distinctive for the grayling also appear in related families.

The Salmonidae are most easily separated from the Argentinidae, Osmeridae, and Plecoglossidae by having 3 rather than 1 or 2 upturned caudal vertebrae. In possessing 3 upturned caudal vertebrae, the Salmonidae, show a closer affinity to the basic isospondylous stock such as the Elopidae and Albulidae. *Elops saurus* and *E. affinis* have 4 upturned caudal vertebrae (Pl. 15, D). *Megalops atlantica* Valenciennes also has 4, whereas the adult of *Albula vulpes* (Linnaeus) has 2 upturned centra (Hollister, 1936).

A combination of characters which are peculiar to the trouts, whitefishes, and graylings, suggest that this is a single circumscribed group and that *Thymallus* is as much a part of it as any of the genera described. First, the 3 subfamilies possess a number of primitive characters in common. These include soft fin rays, cycloid scales, an open pneumatic duct, an adipose fin, the maxilla forming part of the margin of the gape, numerous branchiostegal rays, parapophyses not co-ossified with the centra, oviducts incomplete, and the 3 upturned vertebrae in the caudal skeleton.

Second, certain characters which might be expected to accentuate divergence among groups, tend instead to show relationship. For example, vertebral counts in each of 16 species of salmonid fishes (7 genera) indicate that despite the presence of apparently reliable differences between some species, the variation is gradual and overlapping, rather than abrupt, among species and among genera (Table IV).

The sagitta, the largest of the 3 otoliths, was examined for differences of higher taxonomic significance (Pl. 16). Again the variation is such that the otoliths are of little systematic value.

Svårdson (1945) attempted to use chromosome number in taxonomic studies. He found that in salmonoid fishes the chromosome number varied as follows:

Species	Diploid number of chromosomes
<i>Salmo salar</i>	60
<i>S. trutta</i>	80
<i>Salvelinus alpinus</i>	80
<i>S. fontinalis</i>	84
<i>Coregonus lavaretus</i>	80
<i>C. albula</i>	80
<i>Thymallus thymallus</i>	102
<i>Osmerus eperlanus</i>	58

Although studies of chromosome counts are inconclusive, the data accumulated to the present indicate that there is much overlap and continuous variation. Thus, the pattern of variation in vertebral count (Table IV), the similarity of the otoliths (Pl. 16), and the chromosomal number (Svårdson, 1945) lend support to the hypothesis that the Salmonidae are composed of 3 interrelated groups.

Third, very few of the characters which appear to have value in tracing the evolutionary history of the group (Table V) seem to be diagnostic of a particular genus or even a subfamily. A study of Table V reveals that 3 characters are more fundamental than the others; the absence of an orbitosphenoid bone, the lack of teeth on the maxilla, and the separation of the parietals by the supraoccipital. All 3 are considered specialized traits which foreshadow characters common to the spiny-rayed fishes. If the absence of an orbitosphenoid is used as the basis for separating the 3 groups, then the Thymallinae stand apart from the Coregoninae and Salmoninae. When the edentulous maxilla is used as the primary character the Coregoninae stand alone while the Thymallinae and Salmoninae are grouped together. The broad separation of the parietals by the supraoccipital is diagnostic of the Salmoninae; the Coregoninae and Thymallinae fall into a single category. Since the subfamilies have much in common and assuming these 3 characters are subequal in value, it seems illogical to choose any one feature as diagnostic at a particular taxonomic level. Thus, the unequal emphasis placed on the absence of the orbitosphenoid (Berg, 1940) resulted in the recognition of the graylings as a family, the other groups as subfamilies of the Salmonidae. For the above reasons the trouts, graylings, and whitefishes are placed in a single family, the Salmonidae.

Although the evidence is meager, certain characteristics of the salmonines indicate that they are nearest to the basic salmonid type. This hypothesis is suggested by the following facts: (1) The jaws and mouth are of the generalized pattern typical of numerous other predaceous fishes. It is unlikely that the large, well toothed maxilla was derived from a small, toothless bone such as that of *Coregonus*. *Stenodus leucichthys* is a large-mouthed predaceous fish in which the maxilla borders the gape, yet that bone remains toothless. If teeth once lost could be regained, it seems that this would have occurred in *Stenodus*. (2) The basibranchial plate is probably an old character which has survived in the evolution of the order. In addition to the Salmoninae and *Prosopium* it is present in the Osmeridae and Plecoglossidae (Chapman, 1941a, 1942) and in the Elopidae, Albulidae, and Clupeidae (Ridewood, 1904a, 1904b). (3) The absence of an orbitosphenoid (as in *Thymallus*) is believed to be a recent specialization (Gregory 1933). This bone is large and well developed in the salmonines, as well as in more primitive teleosts such as the Elopidae, Albulidae, and Amiidae. The absence of a basibranchial plate and an orbitosphenoid in *Thymallus* eliminates the modern grayling from consideration as a possible ancestral type of the family (Fig. 2). The chief feature of the Salmoninae in which the entire group is more specialized than the Thymallinae and the Coregoninae is in the separation of the parietals by the supraoccipital. This character has presumably developed since the segregation of the subfamilies.

TABLE V. Characters of chief taxonomic importance in the Salmonidae.

Character	Thymallinae	Coregoninae	Salmoninae
Orbitosphenoid	Absent	Present, small to large	Present, large
Hypethmoid	Absent	Present	Usually absent, occasionally present in <i>Salvelinus fontinalis</i> and in <i>Salmo trutta</i>
Basisphenoid	Present	Usually present, sometimes absent in <i>Coregonus</i>	Present
Parietal Bones	Meeting along midline	Meeting along midline in <i>Coregonus</i> and <i>Prosopium</i> narrowly separated in <i>Stenodus</i>	Separated by supraoccipital
Basibranchial plate	Absent	Present in <i>Prosopium</i> ; absent in <i>Coregonus</i> and <i>Stenodus</i>	Present
Dermosphenotic	Present	Present	Absent
Suprapreopercle	Absent	Absent	Present
Median (third) extrascapular on nape	Present	Absent	Usually absent; occasionally present in <i>Salvelinus namaycush</i> and <i>S. fontinalis</i>
Postorbitals	In contact with preopercle	In contact with preopercle, except in <i>Stenodus</i>	Not in contact with preopercle, except in <i>Oncorhynchus</i>
Teeth on maxillae	Present	Absent	Present
Jaw articulation	Below eye or at posterior margin	Below eye	Behind eye; below in <i>Brachymystax</i>
Teeth size	Intermediate	Small or absent	Intermediate to large
Number of epurals	Two	Two	Two or three
Epipleurals	Present anteriorly	Absent	Usually absent, occasionally present anteriorly in <i>Salvelinus fontinalis</i>
Dorsal fin rays (including anterior rudiments)	17 to 25	10 to 15	11 to 16
Scale size and shape	Moderate; with anterior margin fluted	Moderate; with anterior margin round or wavy	Small; with anterior margin round
Parr marks (in young)	Present	Usually absent; present in some species of <i>Prosopium</i>	Usually present; absent in <i>Oncorhynchus gorbuscha</i>
Egg size	Small	Small	Usually large; small in <i>Brachymystax</i>

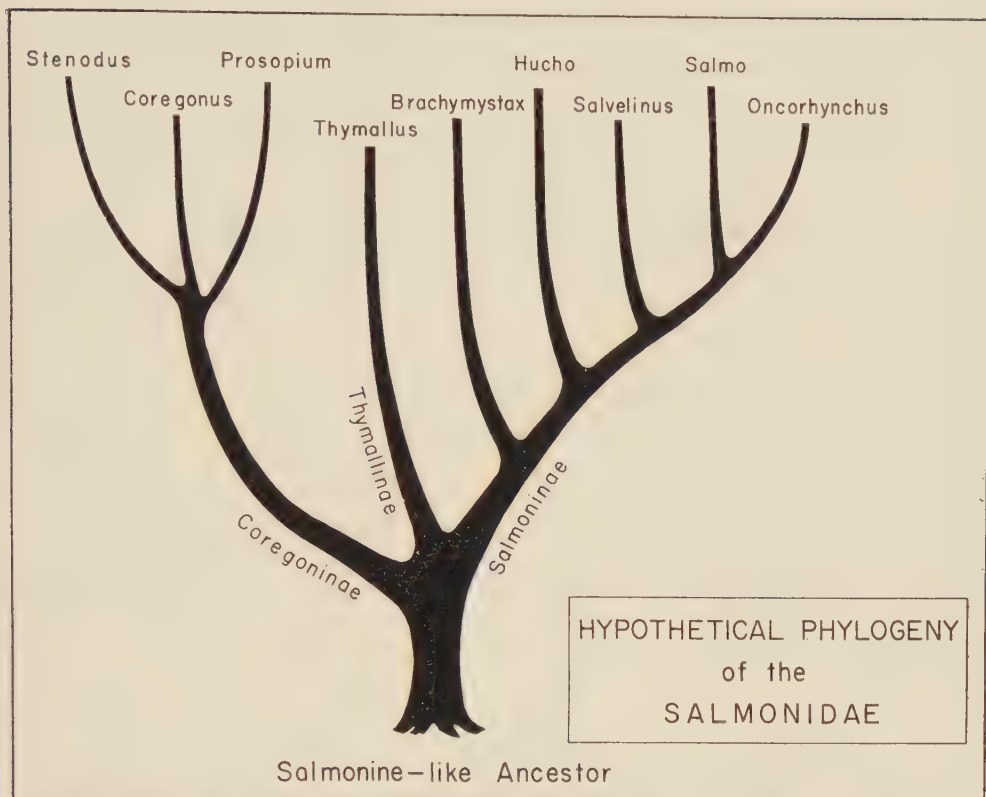


FIG. 2. Hypothetical phylogeny of the Salmonidae.

Among the Salmoninae, *Brachymystax lenok* appears to possess characters closest to the ancestral form of the family. The salmonine features are present but are not strongly developed. For example, *Brachymystax* has a medium-sized mouth, only slightly larger than that in *Thymallus*. Teeth of moderate size are well developed on the maxilla. *Brachymystax* is the only salmonine which produces small ova. One can conceive of an ancestral form like *Brachymystax*, but with the parietals meeting in the midline, evolving into a large-mouthed predaceous *Salmo*, into a weak-jawed insectivorous *Thymallus*, or in still another direction, into a small-mouthed, toothless, plankton-feeding *Coregonus*.

From a *Brachymystax*-like ancestor a salmonine evolutionary trend has probably been marked by a gradual separation of the parietals by the supra-occipital, the fusion of the dermosphenotic with the pterotic or its independent loss, increase in egg size, and the jaws becoming large and more strongly toothed necessitating the displacement of the jaw hinge to a position behind the orbit.

It is possible that *Salmo* represents a form close to the main line of evolution in the salmonines (Regan, 1920; Nall, 1930; Tchernavin, 1937). *Salmo* has the characteristics named in the above paragraph and, in addition, is distinguished

by its colour pattern (dark spots on a light background), the toothed shaft of the vomer, and the T-shaped pattern of teeth on the roof of the mouth (Fig. 1, E).

Hucho appears to be intermediate between *Brachymystax* and *Salmo* (Fig. 2). It differs from *Salmo* in that the shaft of the vomer is not toothed. Therefore, the palatine and vomerine teeth form an oval pattern on the roof of the mouth similar to that of *Brachymystax* (Fig. 1, B and C).

Oncorhynchus is likely a more recent offshoot from *Salmo* (Fig. 2). Although specializations involving habits, physiology, and skeletal characters are well marked in the adult, these are not so pronounced in the young. Thus, some of the characters which Tchernavin (1937: 239, 1938a: 164) used to separate *Oncorhynchus* from *Salmo* are found to be similar in the juveniles of both genera. In juvenile *Oncorhynchus*, dorsal fontanelles are present, the ascending process of the premaxilla is about equally well developed in the two genera, there is little difference in the shape of the supraethmoid, and the arrangement of the teeth is similar. Innovations which characterize *Oncorhynchus* and thus separate it from *Salmo*, at least in the adult, are the backward extension of the postorbitals to touch the preopercle, an anteroventral extension of the opisthotic to touch the prootic, the closure of the dorsal fontanelles, the azygous form of the cartilaginous rostrum, the wide gap between the palatine and vomerine teeth on the palate (Fig. 1, F), and the simultaneous ripening of all germ cells.

Salvelinus may represent a rather early split from the stem form (Fig. 2). It has a distinctive colour pattern and the scales are slightly more specialized than in *Salmo* (Morton and Miller, 1954: 210). Osteological characteristics include the edentulous shaft on the vomer, the length and shape of the supraethmoid (Pl. 12, J), and the elongate ascending process on the premaxilla (Pl. 9, B).

The coregonines are believed to represent an early offshoot of a salmonine-like ancestor (Fig. 2). This separation occurred before the parietals became widely separated by the supraoccipital. It also antedated the loss of the dermosphenotic and (usually) the hypethmoid bones, both of which are well developed in the whitefishes. As indicated on page 747, it does not seem likely that the evolutionary process went the other way (Coregoninae to Salmoninae).

The Coregoninae are of interest because of their adaptive modifications for particular feeding habits. They also afford examples of parallel evolution. If the coregonines evolved from an ancestor similar to *Brachymystax*, they came from an insectivorous or piscivorous type with well-developed jaws. The first step in its evolution was either toward planktonic feeding, presumably involving development of numerous, long gill rakers, or toward bottom (detritus) feeding in which the mouth became small and the gill rakers remained short. In either event maxillary teeth were lost and those on the other jaw bones were reduced in number and strength.

Prosopium may be nearest the ancestral type since it shares two primitive characters with the trouts: parr marks are known to occur in at least some species and a basibranchial plate is present. The evolution of *Coregonus* and *Stenodus*

is marked by the loss of the basibranchial plate and parr marks. *Stenodus leucichthys*, therefore, is a whitefish which has evolved trout-like feeding habits necessitating a large mouth, strong jaws, and teeth. Since large canine teeth were perhaps irrevocably lost the new dentition features numerous, small pointed teeth on the tongue, palate, and in the skin covering the gill arches.

That *Prosopium* could have given rise to a plankton-feeding form with numerous long gill rakers is borne out by *P. gemmiferum*. That this species is a *Prosopium*, likely evolved at a much later date, is indicated by the presence of a basibranchial plate and the similarity of the supraethmoid bone (Pl. 12, C, D, and G).

The "cisco type" (*leucichthys*-group of Gasowska, 1960) has specialized in planktonic feeding and may have given rise to the bottom-feeding forms (*Coregonis clupeaformis* and *C. nasus*), although there is no evidence for this. The reverse evolutionary trend may have occurred with the small-mouthed, bottom-feeding species being ancestral to the planktonic forms, paralleling the evolution of *Prosopium gemmiferum* from a bottom-feeding *Prosopium*. The coregonids exhibit a great deal of plasticity (Smith, 1957) and thus their ancestry is not clear. That *Coregonus clupeaformis* and *C. nasus* are not in the direct line of evolution to *Prosopium* is indicated because they lack a basibranchial plate, have no parr marks, and the supraethmoid is short and triangular rather than elongate and straight (Pl. 12, A, C, and D).

This study reveals that *Stenodus leucichthys* is more closely allied to *Coregonus* than has heretofore been realized (Tchernavin, 1923, placed *Stenodus* in a separate subfamily). However, *Stenodus* Richardson is considered to be a distinct genus (Fig. 2) and differs from *Coregonus* and *Prosopium* in the following features: The orbital ring is closed through enlargement of the first supraorbital and the dermosphenotic; the postorbitals do not touch the preopercle; the mouth is large; the orbitosphenoid is large; the vomer and palatine bear numerous teeth (Pl. 11); the teeth on the dentary and premaxilla are persistent (Pl. 11); the bones are large and heavy; and there are more branchiostegal rays, (9) 10-11 (12) (Fuller, 1955).

The genus *Prosopium* Milner represents an earlier evolutionary line than either *Stenodus* or *Coregonus* and may be distinguished by the following features: A basibranchial plate is present; there is a single narial flap; parr marks are present in the young, of those species for which young are known; the first supraorbital is short; and the supraethmoid is long and narrow (Pl. 12, C, D, and G).

The genus *Coregonus* Linnaeus may be distinguished from both *Stenodus* and *Prosopium* only in that the first supraorbital is intermediate in length. In other characters it agrees with one or the other genus (see above).

Although there are fewer differences between *Prosopium* and *Coregonus* than between either one and *Stenodus*, those that distinguish *Prosopium* from the other groups are judged the more fundamental. As additional evidence on this, *Coregonus* × *Stenodus* hybrids are known (Berg, 1948), but no hybrids involving

Prosopium have been reported. The phyletic separation of *Prosopium* is thus believed to be somewhat older than that between *Coregonus* and *Stenodus* (Fig. 2).

Thymallus may be visualized as descended from a salmonid ancestor (Fig. 2) similar to the recent *Brachymystax* but with the parietals meeting at the midline and with a dermosphenotic bone. The size of the mouth, the location of the jaw hinge, and the dentition on the roof of the mouth (Pl. 13, A and B) are not very different in these genera. The orbitosphenoid is sporadically lacking throughout the suborder Salmonoidei (Plecoglossidae, Osmeridae). The suprapreopercle has been lost also in the Coregoninae, and the dermosphenotic retained in both that subfamily and the Thymallinae. The loss of the epipleurals is not complete in the Salmoninae (e.g., *Salvelinus fontinalis*), and their presence in *Thymallus* may indicate the retention of an old character. The dorsal fin with 17 or more rays, only one more than the maximum in the Salmoninae, is of limited significance and probably is a rather recent acquisition.

I believe the Salmonidae are descended from an ancestral type which had many of the modern salmonine characteristics. However, they have diverged, perhaps during or after the Miocene, into 3 phyletic lines, which are here considered subfamilies. A hypothetical arrangement of the genera of the family Salmonidae is shown in Fig. 2.

SUMMARY

Suborder Salmonoidei (order Clupeiformes), comprising the families Salmonidae, Argentinidae, Osmeridae, Plecoglossidae, Retropinnatidae, Salangidae and Aplochitonidae, has the following characters: Parapophyses not fused to the centra; autogenous haemal processes in the posterior caudal vertebrae; oviducts absent or incomplete; adipose fin usually present; neural and haemal arches and spines of caudal skeleton laterally compressed; and photophores absent.

Family Salmonidae differs from one or more of the other salmonoid families in each of the following: Three upturned caudal vertebrae (unique in Salmonidae); autogenous neural processes in the posterior caudal vertebrae; mesopterygoid toothless (toothed in Osmeridae and Plecoglossidae, absent in Salangidae); 3 postcleithra (absent in Plecoglossidae); mesocoracoid present (absent in Retropinnatidae and Aplochiochitonidae); opisthotic present (absent in Retropinnatidae, Aplochitonidae, and Salangidae); scapular foramen entirely contained within the scapula (not in Plecoglossidae); and pyloric caeca many (11 or more).

The subfamilies and genera of the Salmonidae may be defined as follows: Subfamily Salmoninae consists of salmonid fishes with an orbitosphenoid, suprapreopercle, and basibranchial plate; no dermosphenotic; usually no hypethmoid and epipleurals; not more than 16 dorsal-fin rays; small rounded scales; large-toothed maxilla and premaxilla; usually large ova and no postlarval stage; young usually with parr marks; and parietals separate at the midline.

Five genera are recognized:

Genus *Brachymystax*. Salmonine fishes with relatively small mouth, jaw hinge below posterior margin of eye; no teeth on shaft of vomer; U-shaped band of palatine and vomerine teeth; postorbitals not in contact with preopercle; long supraethmoid with numerous posterior projections; intermediate-sized ascending process of premaxilla; opisthotic not touching prootic; persistent dorsal fontanelles; and small ova.

Genus *Hucho*. Salmonine fishes with large mouth, jaw hinge behind orbit; no teeth on shaft of vomer; U-shaped band of palatine and vomerine teeth; postorbitals not in contact with preopercle; broad supraethmoid, with numerous small posterior projections; intermediate-sized ascending process of premaxilla; opisthotic not touching prootic; persistent dorsal fontanelles; and large ova.

Genus *Salvelinus*. Salmonine fishes with large mouth, jaw hinge well behind orbit; no teeth on shaft of vomer; narrowly separated palatine and vomerine teeth; postorbitals not in contact with preopercle; long supraethmoid with numerous posterior projections; extended and well-developed ascending process of premaxilla; opisthotic not touching prootic; dorsal fontanelles persistent; pattern of light spots on a dark background; and large ova.

Genus *Salmo*. Salmonine fishes with large mouth, jaw hinge behind orbit; teeth on shaft of vomer; narrowly separated palatine and vomerine teeth; postorbitals not in contact with preopercle; supraethmoid notched posteriorly; intermediate-sized ascending process of premaxilla; opisthotic not touching prootic; dorsal fontanelles persistent; pattern of dark spots on a light background; and large ova.

Genus *Oncorhynchus*. Salmonine fishes with large mouth; jaw hinge behind orbit; teeth on shaft of vomer; widely separated palatine and vomerine teeth; postorbitals contacting preopercle; in the adult supraethmoid deeply notched posteriorly; no ascending process of premaxilla; opisthotic touches prootic; in adult no dorsal fontanelles; and large ova.

Subfamily Thymallinae is composed of salmonid fishes with no orbitosphenoid, hypethmoid, suprapreopercle, or basibranchial plate; with epipleurals and dermosphenotic; 17 or more dorsal-fin rays; scales whose embedded margins are indented; toothed maxilla and premaxilla; small ova and a postlarval stage; young with parr marks; and parietals meet at the midline. Subfamily Thymallinae includes a single genus, *Thymallus*.

Subfamily Coregoninae consists of salmonid fishes with an orbitosphenoid, dermosphenotic, and hypethmoid; no epipleurals or suprapreopercle; not more than 15 dorsal-fin rays; large rounded scales; no maxillary teeth; small ova and a postlarval stage; young with or without parr marks; and parietals meet at the midline.

Three genera are recognized, as follows:

Genus *Prosopium*. Light-boned coregonine fishes with an open orbital ring; short first supraorbital; small mouth; a basisphenoid and a basibranchial plate; no or weak teeth; long third postcleithrum; postorbitals in contact with preopercle; elongate supraethmoid; a single nasal flap; and parr marks in known juveniles.

Genus *Coregonus*. Light-boned coregonine fishes having an open orbital ring; intermediate-sized first supraorbital; small mouth; no basibranchial plate; usually a basisphenoid; no or weak teeth; long 3rd postcleithrum; postorbitals in contact with preopercle; short supraethmoid; no parr marks; and 2 nasal flaps.

Genus *Stenodus*. Heavy-boned coregonine fishes with a closed orbital ring; long first supraorbital and dermosphenotic; large mouth; a basisphenoid; no basibranchial plate; persistent jaw teeth; numerous teeth on vomer and palatine; rounded 3rd postcleithrum; postorbitals not in contact with preopercle; short supraethmoid; and 2 nasal flaps.

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PLATES 1-16

PLATE 1

Chondrocranium of *Thymallus arcticus*A. Dorsal view, UMMZ 172465-S, about 1.7 $\times$ B. Ventral view, UMMZ 172465-S, about 1.7 $\times$

Abbreviations.—BOC, basioccipital; BS, basisphenoid; DF, dorsal fontanelle; EOC, exoccipital; EPO, epiotic; OPO, opisthotic; PF, prefrontal; PRO, prootic; PS, pterosphenoid; PTO, pterotic; SOC, supraoccipital; SPO, sphenotic.

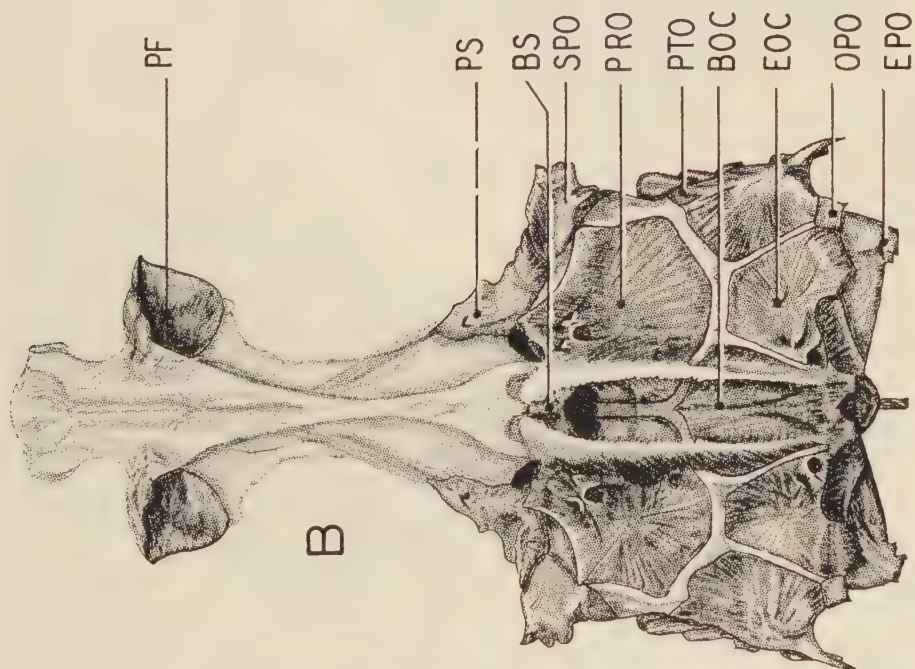
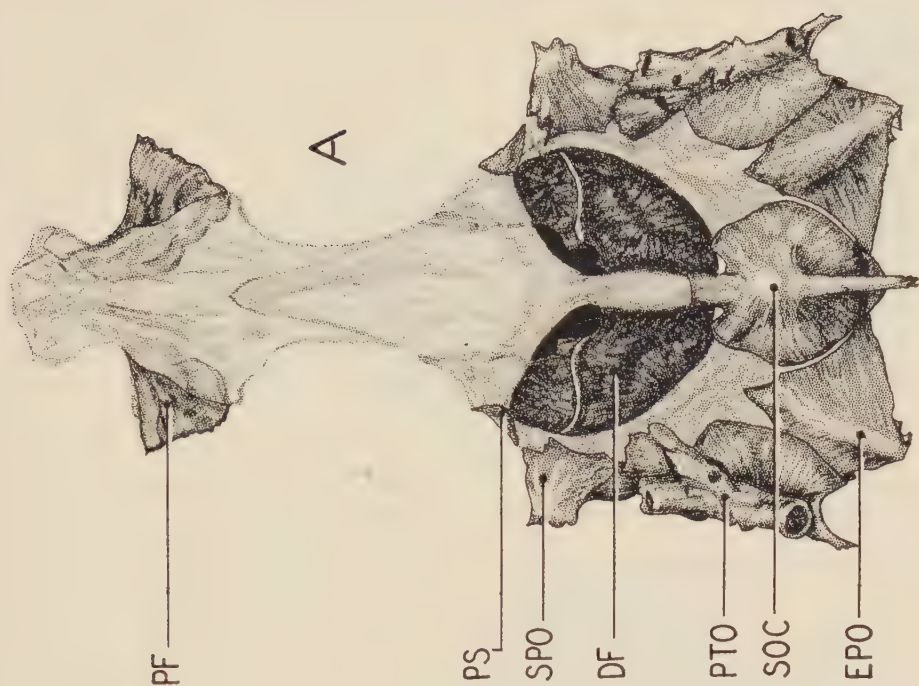


PLATE 2

Chondrocranium of *Thymallus arcticus*

- A. Lateral view, UMMZ 172465-S about 1.7 $\times$
- B. Posterior view, UMMZ 172465-S about 1.7 $\times$
- C. Mesial view, UMMZ 172465-S about 1.7 $\times$

Abbreviations.—BOC, basioccipital; BS, basisphenoid; DF, dorsal fontanelle; EOC, exoccipital; EPO, epiotic; FM, foramen magnum; OPO, opisthotic; PF, prefrontal; PRO, prootic; PS, pterosphenoid; PTO, pterotic; SOC, supraoccipital; SPO, sphenotic.

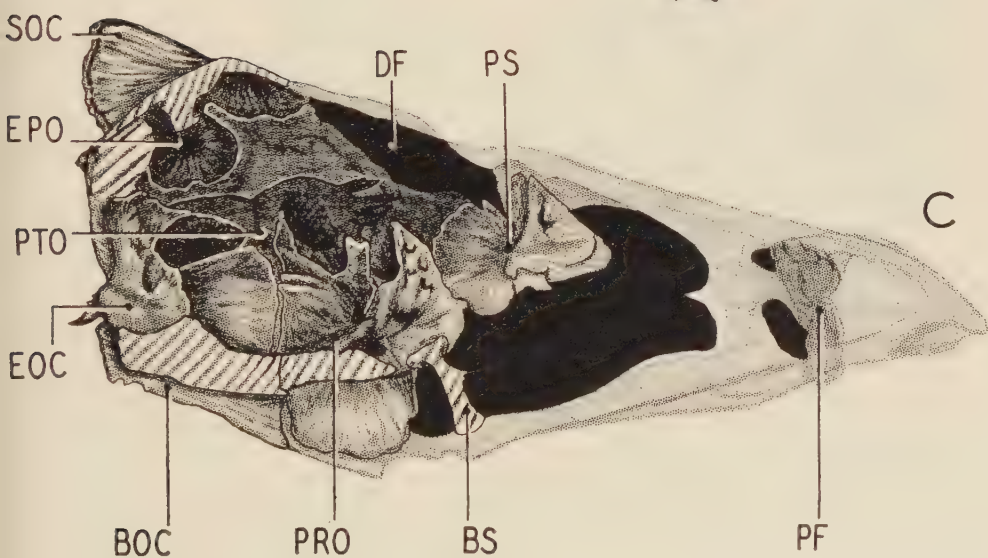
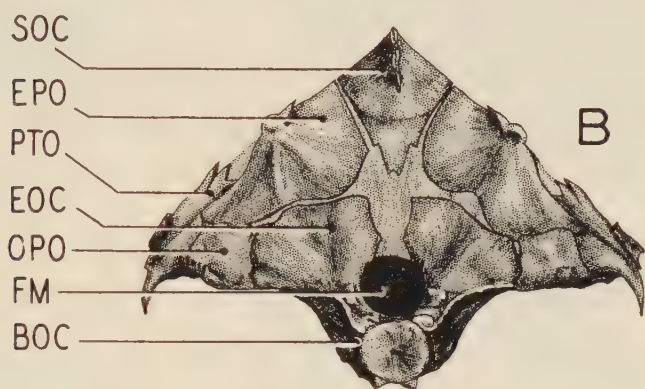
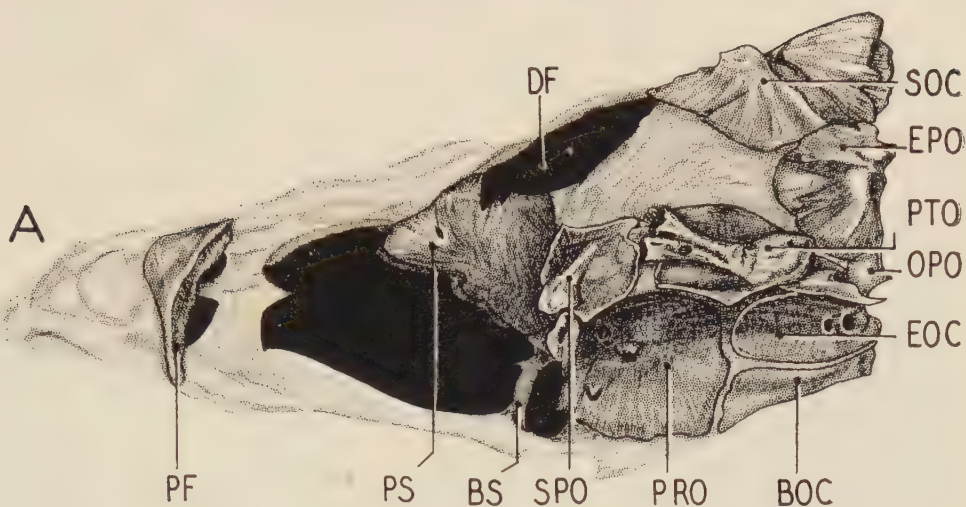


PLATE 3

Dorsal views of chondrocrania of Salmonidae

A. *Coregonus artedii*. UMMZ 172466-S, about 1.6 ×

B. *Salvelinus namaycush*. UMMZ 172463-S, about 1.6 ×

Abbreviations.—DF, dorsal fontanelle; EOC, exoccipital; EPO, epiotic; HE, hypethmoid; OPO, opisthotic; PF, prefrontal; PS, pterosphenoid; PTO, pterotic; SOC, supraoccipital; SPO, sphenotic.

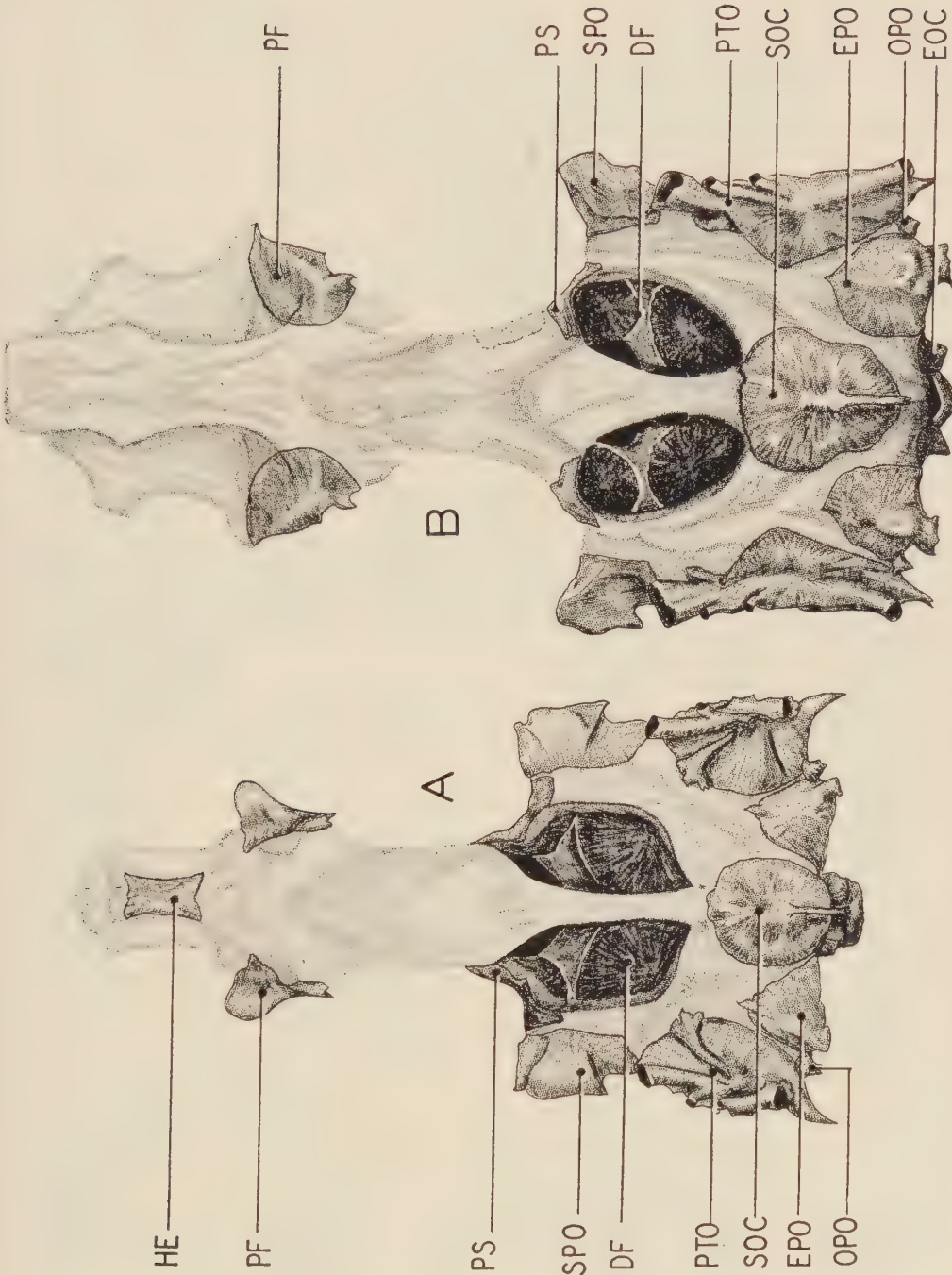


PLATE 4

Dermal skull bones of *Thymallus arcticus*

UMMZ 172465-S, about 0.8 ×

Abbreviations.—A, angular; D, dentary; DS, dermosphenotic; ES, extrascapular; F, frontal; IO, infraorbital; IOP, interopercle; LA, lachrymal; M, maxilla; N, nasal; OP, opercle; P, parasphenoid; PA, parietal; PM, premaxilla; PO, postorbital; POP, preopercle; RA, retroarticular; SE, supraethmoid; SM, supramaxilla; SO, supraorbital; SOP, subopercle; V, vomer.

PLATE 5

Hyoid arch and lower jaw of *Thymallus arcticus*

UMMZ 172465-S, about 1.3 ×

Abbreviations.—A, angular; BB, basibranchial; BH, basihyal; CH, ceratohyal; CM, coronomeckelian; D, dentary; ECT, ectopterygoid; EH, epihyal; HH, hypohyal; HY, hyomandibular; IH, interhyal; LP, lingual plate; MC, Meckel's cartilage; MES, mesopterygoid; MET, metapterygoid; PAL, palatine; PQ, palatoquadrate; Q, quadrate; RA, retroarticular; SY, symplectic; U, urohyal.

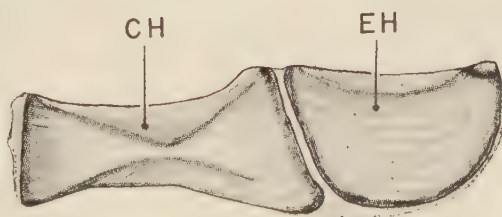
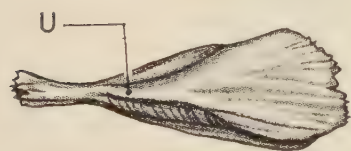
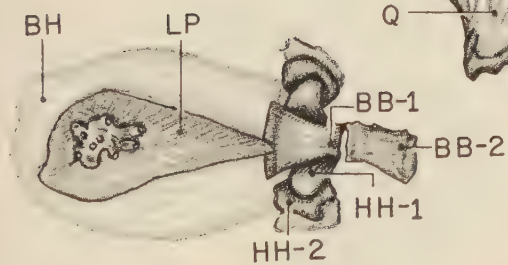
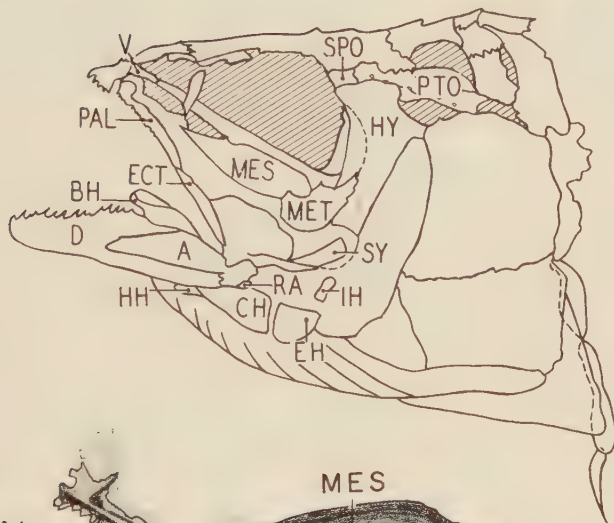
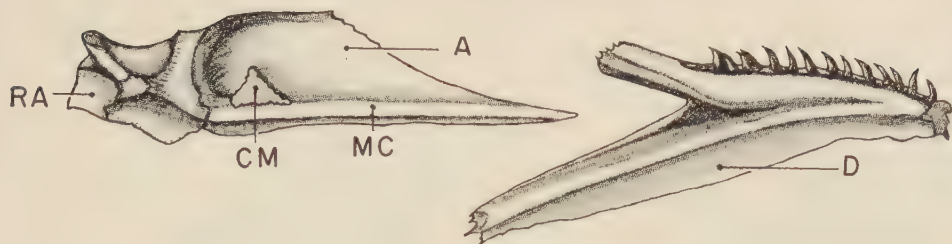


PLATE 6

Branchial skeletons of Salmonidae

- A. *Prosopium cylindraceum*, UMMZ 59728, about 1.6 ×
- B. *Salvelinus fontinalis*, UMMZ 85467, about 1.1 ×
- C. *Thymallus arcticus*, UMMZ 167092, about 1.1 ×
- D. *Coregonus clupeaformis*, UMMZ 75327, about 1.3 ×

Abbreviations.—BB, basibranchial; BP, basibranchial plate; CB, ceratobranchial; EB, epi-branchial; HB, hypobranchial; HH, hypohyal; LP, lingual plate; PB, pharyngobranchial; PP, pharyngeal plate.

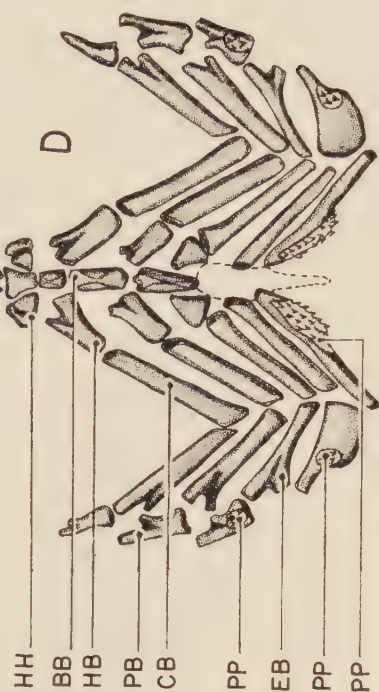
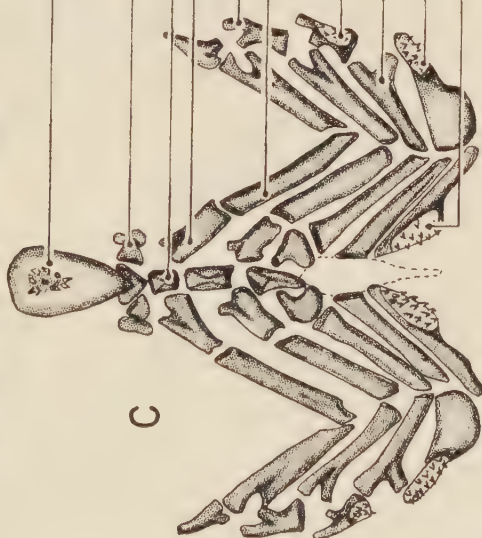
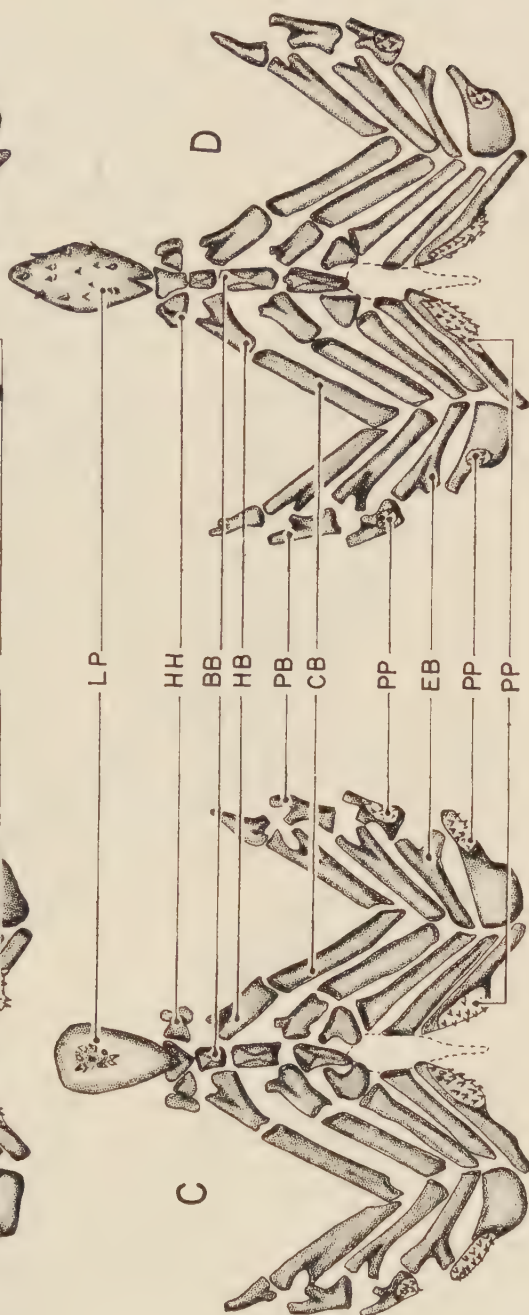
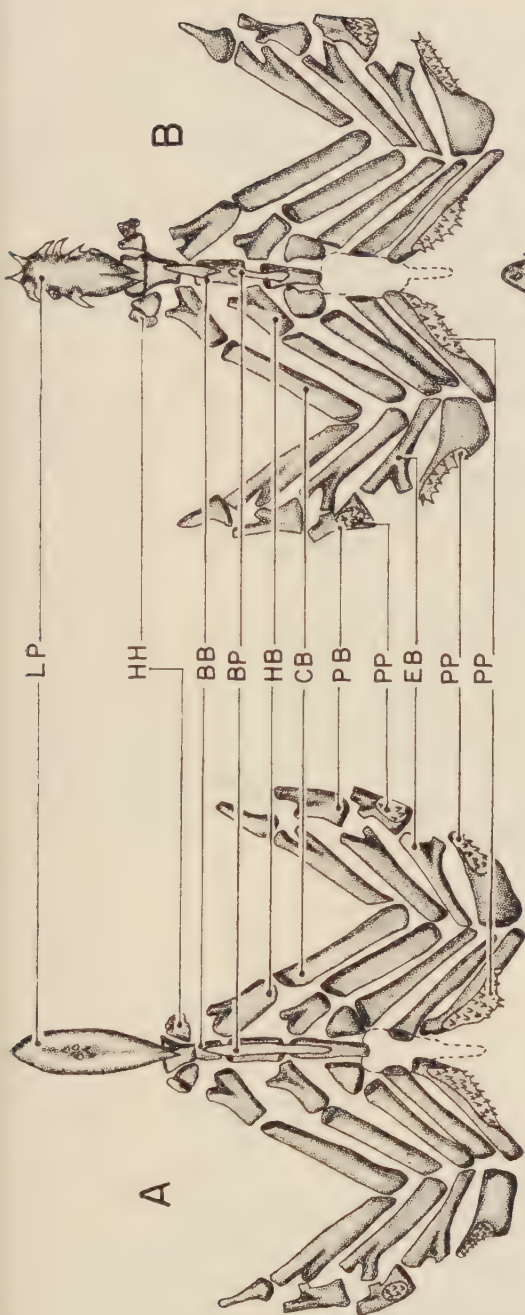


PLATE 7

Axial skeleton and pelvic girdle of *Thymallus arcticus*

- A. Trunk vertebrae nos. 8, 9, and 10,
UMMZ 167092, about 1.3 $\times$
- B. Caudal vertebrae nos. 45, 46, 47, and 48,
Ptergiophores of anal fin nos. 9, 10, 11, and 12,
Anal fin rays nos. 11, 12, 13, 14, and 15,
UMMZ 167092, about 1.4 $\times$
- C. Caudal skeleton, UMMZ 167092, about 1.4 $\times$
- D. Pelvic girdle, UMMZ 167092, about natural size

Abbreviations.—AFR, anal fin ray; BPTG, basipterygium; C, centrum; E, epural; EHS, expanded haemal spine; EN, epineural; ENS, expanded neural spine; EP, epipleural; H, hypural; HA, haemal arch; HS, haemal spine; IN, interneural; NA, neural arch; NS, neural spine; PAP, parapophysis; PFR, pelvic fin ray; POZ, postzygapophysis; PRZ, prezygapophysis; PTG, ptergiophore; R, rib; UN, uroneural; US, urostyle.

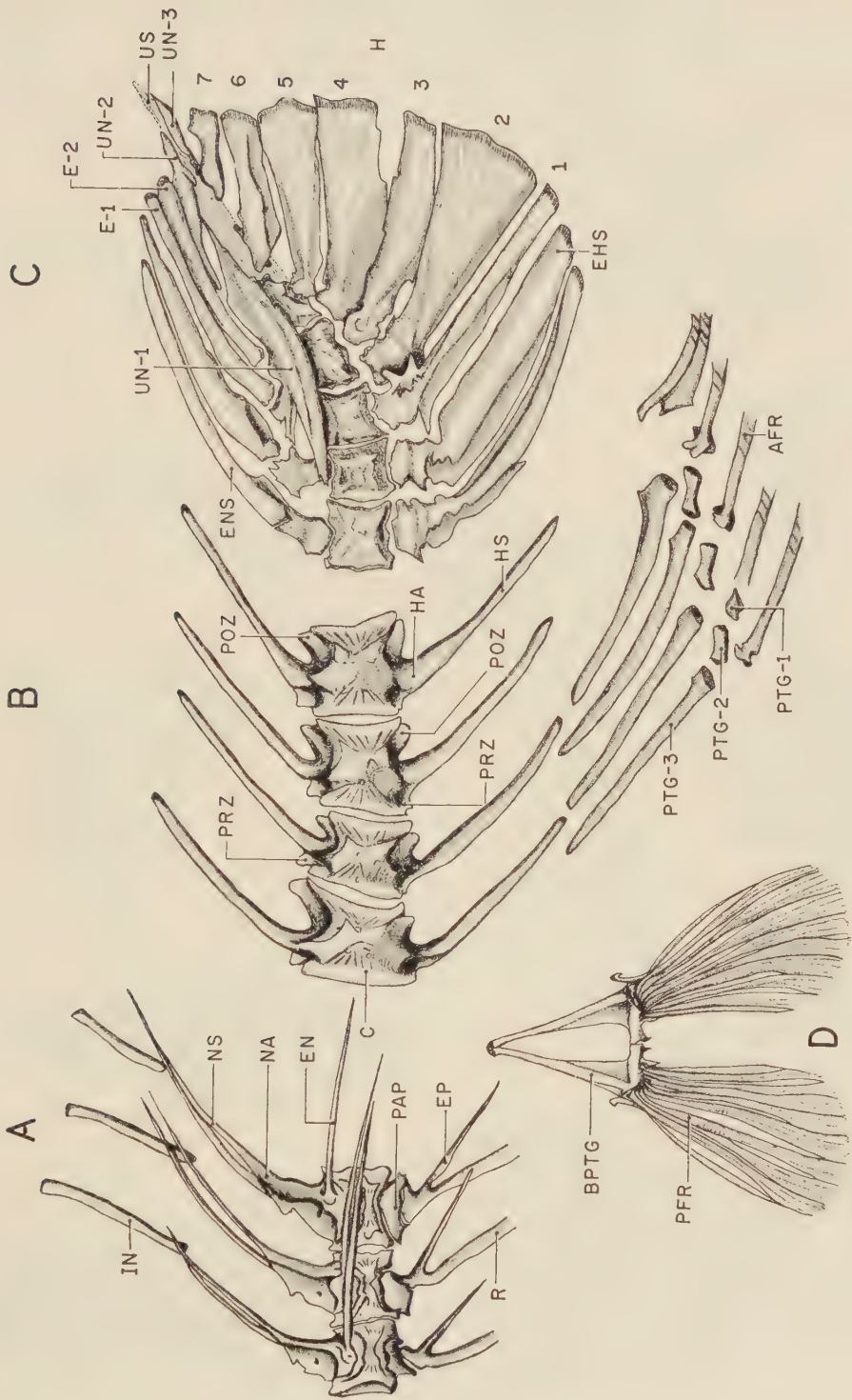


PLATE 8

Pectoral girdle of *Thymallus arcticus*A. Mesial view, UMMZ 172465, about 0.4 $\times$ B. Lateral view, UMMZ 172465, about 0.4 $\times$ Disarticulated skeleton, UMMZ 167092, about 2.6 $\times$

Abbreviations.—AC, actinost; CC, coracoid; CL, cleithrum; MSC, mesocoracoid; PCL, postcleithrum; PT, posttemporal; S, scapula; SCL, supracleithrum.

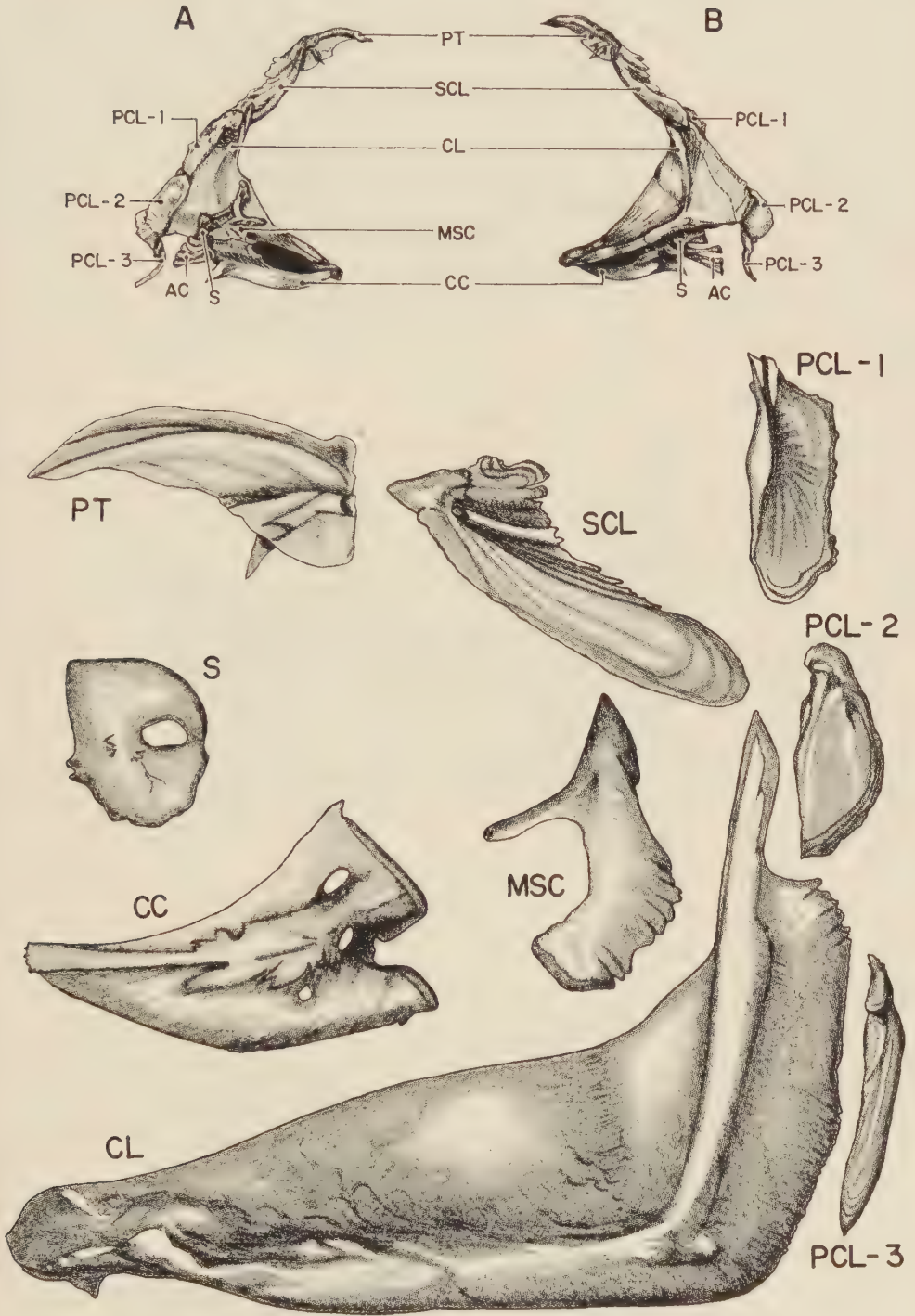
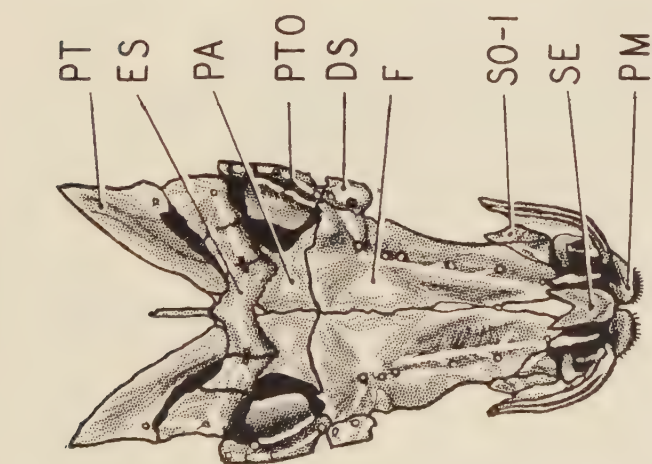


PLATE 9

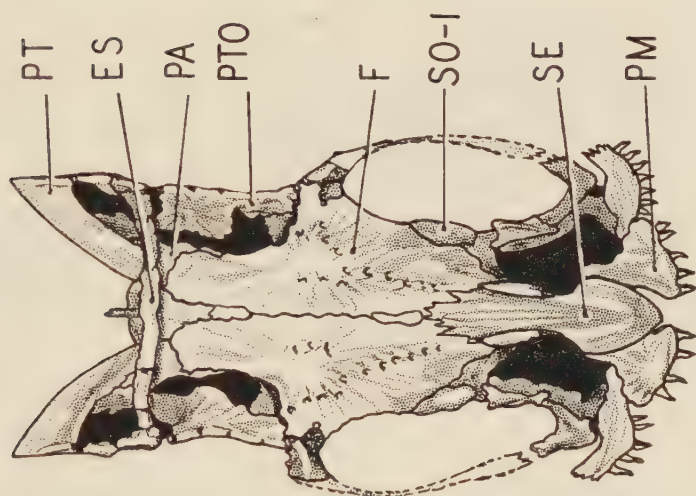
Dorsal view of skulls of Salmonidae

- A. *Thymallus arcticus*, UMMZ 172465-S, about 0.8 $\times$
- B. *Salvelinus namaycush*, UMMZ 172463-S, about 0.7 $\times$
- C. *Coregonus artedii*, UMMZ 172467-S, about 0.9 $\times$

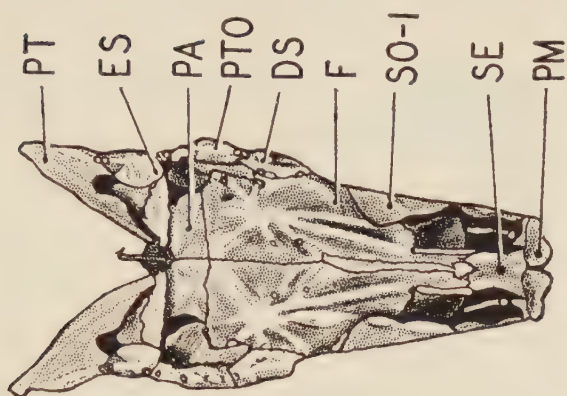
Abbreviations.—DS, dermosphenotic; ES, extrascapular; F, frontal; PA, parietal; PM, premaxilla; PT, posttemporal; PTO, pterotic; SE, supraethmoid; SO, supraorbital.



A



B



C

PLATE 10

Lateral views of skulls of Salmonidae

A. *Coregonus artedii*, UMMZ 172467-S, about 0.36 $\times$

B. *Thymallus arcticus*, UMMZ 172465-S, about 0.36 $\times$

C. *Salvelinus namaycush*, UMMZ 172464-S, about 0.27 $\times$

Abbreviations.—A, angular; BR, branchiostegal ray; D, dentary; DS, dermosphenotic; ES, extrascapular; HY, hyomandibular; IO, infraorbital; IOP, interopercle; LA, lachrymal; M, maxilla; N, nasal; OP, opercle; PM, premaxilla; PO, postorbital; POP, preopercle; PTO, pterotic; Q, quadrate; RA, retroarticular; SM, supramaxilla; SO, supraorbital; SOP, subopercle; SP, suprapreopercle; SY, symplectic.

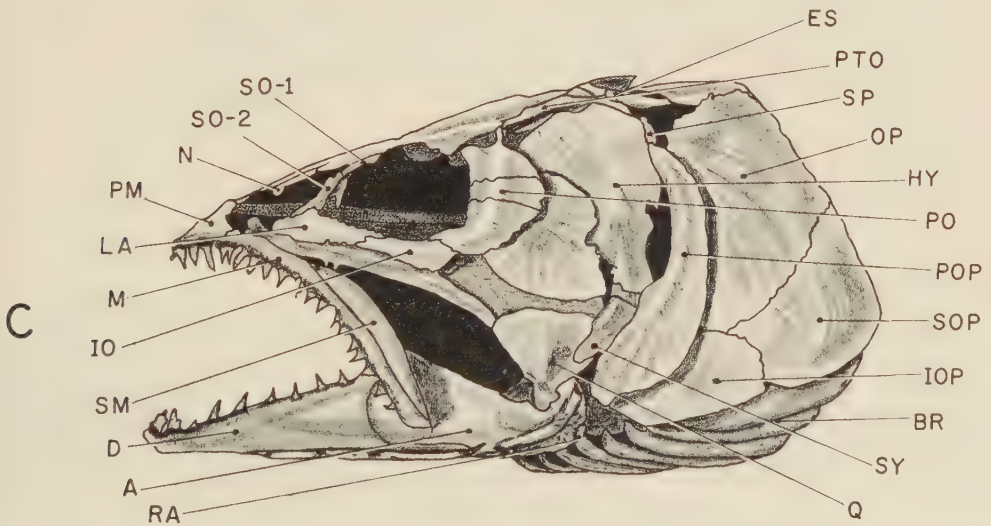
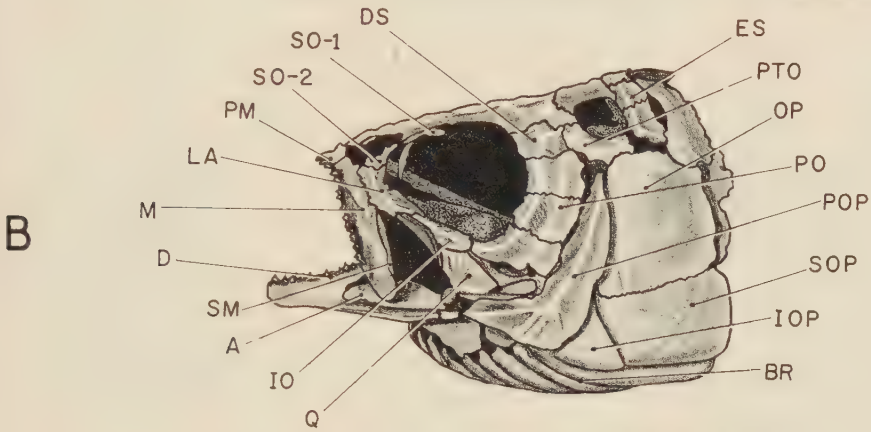
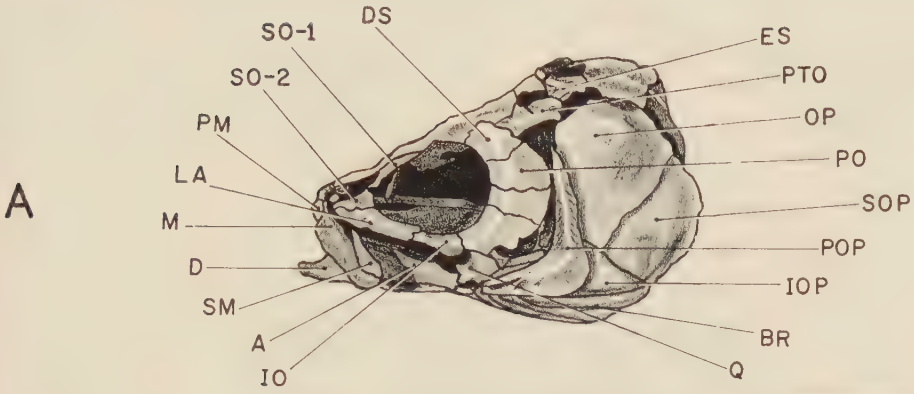


PLATE 11

Selected bones of *Stenodus leucichthys*

Pectoral girdle, mesial view, UMMZ 172487, about 0.6 ×

Vomer, UMMZ 161995, about 2.0 ×

Premaxilla, UMMZ 161995, about 2.0 ×

Supraethmoid, UMMZ 161995, about 2.0 ×

Palatine, UMMZ 161995, about 2.0 ×

Dentary, UMMZ 161995, about 1.5 ×

Abbreviations.—AC, actinost; CC, coracoid; CL, cleithrum; D, dentray; MSC, mesocoracoid; PAL, palatine; PCL, postcleithrum; PM, premaxilla; S, scapula; SE, supraethmoid; V, vomer.

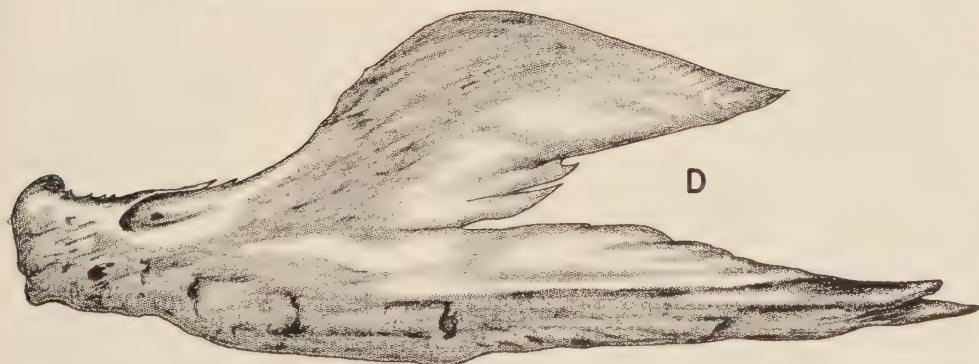
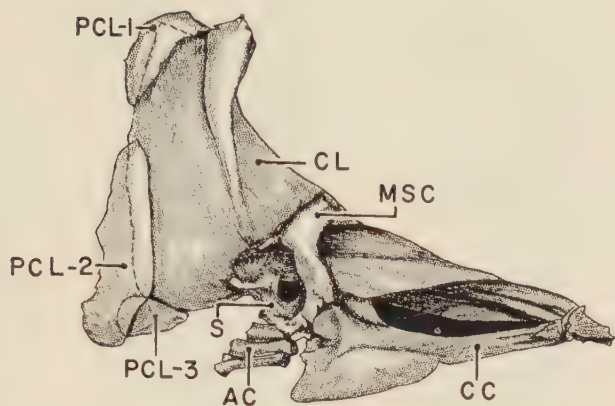


PLATE 12

Supraethmoid bones of Salmonidae

- A. *Coregonus clupeaformis*, UMMZ 75327, about 4.0 ×
- B. *Coregonus artedii*, UMMZ 172467, about 3.2 ×
- C. *Prosopium cylindraceum*, UMMZ 59702, about 2.8 ×
- D. *Prosopium abyssicola*, UMMZ 141811, about 3.0 ×
- E. *Coregonus sardinella*, about 3.3 ×
- F. *Oncorhynchus gorbuscha*, UMMZ 172444, about 1.7 ×
- G. *Prosopium gemmiferum*, UMMZ 141809, about 3.6 ×
- H. *Hucho perryi*, UMMZ 172493, about 1.3 ×
- I. *Brachymystax lenok*, UMMZ 172490, about 1.8 ×
- J. *Salvelinus namaycush*, UMMZ 172463, about 2.0 ×
- K. *Salmo gairdneri*, UMMZ 172468, about 1.7 ×
- L. *Salvelinus fontinalis*, UMMZ 172462, about 1.7 ×

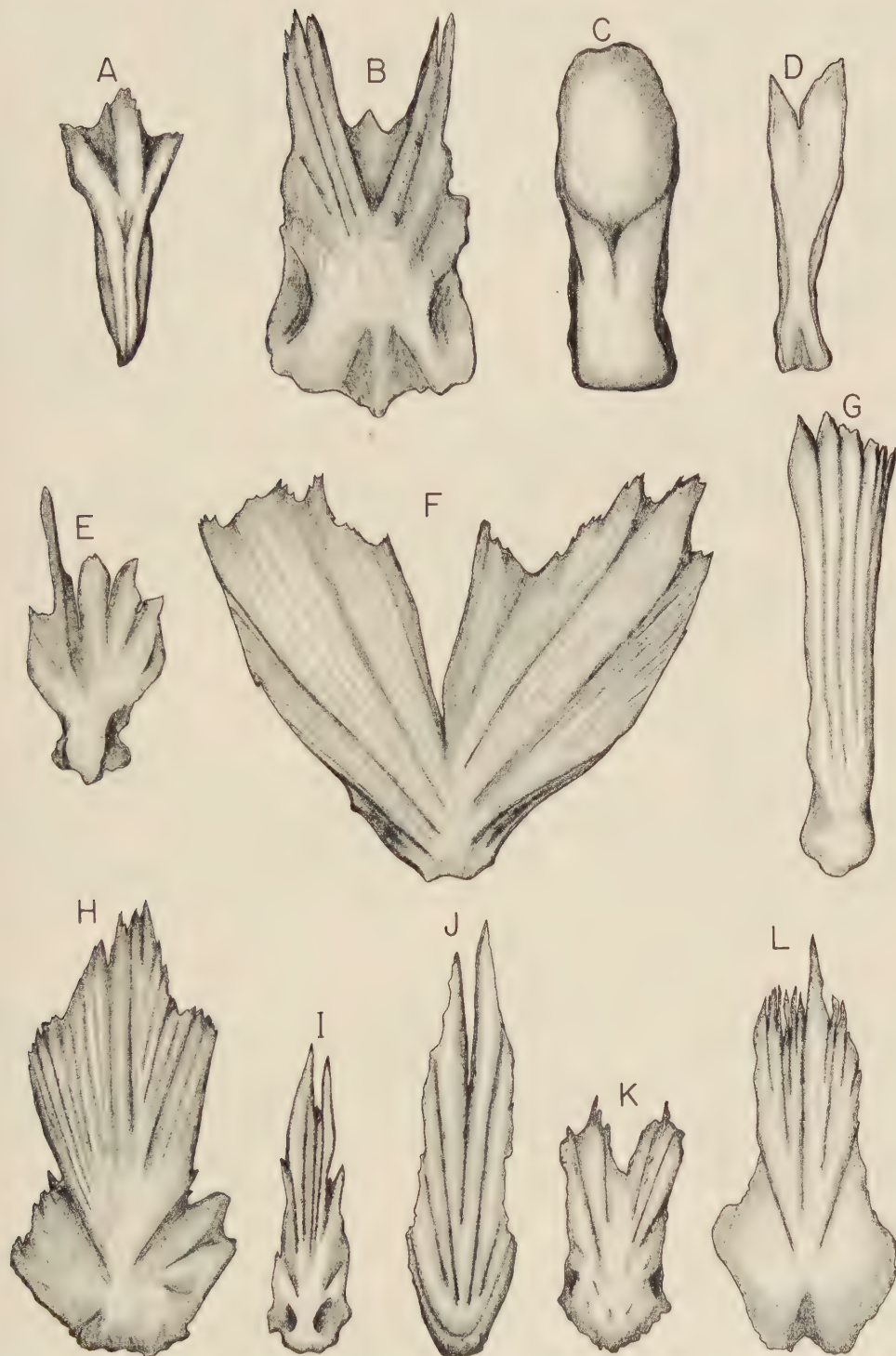


PLATE 13

Upper jaw bones of Salmonidae

- A. *Coregonus nasus*, about 1.1 ×
- B. *Prosopium gemmiferum*, UMMZ 156788, about 1.1 ×
- C. *Salmo trutta*, UMMZ 124553, about 1.9 ×
- D. *Brachymystax lenok*, UMMZ 172490, about 1.1 ×
- E. *Prosopium cylindraceum*, UMMZ 59728, about 1.9 ×
- F. *Stenodus leucichthys*, UMMZ 161995, about 0.6 ×
- G. *Coregonus sardinella*, about 1.1 ×
- H. *Hucho perryi*, UMMZ 172493, about 0.8 ×

Abbreviations.—M, maxilla; PM, premaxilla; SM, supramaxilla.

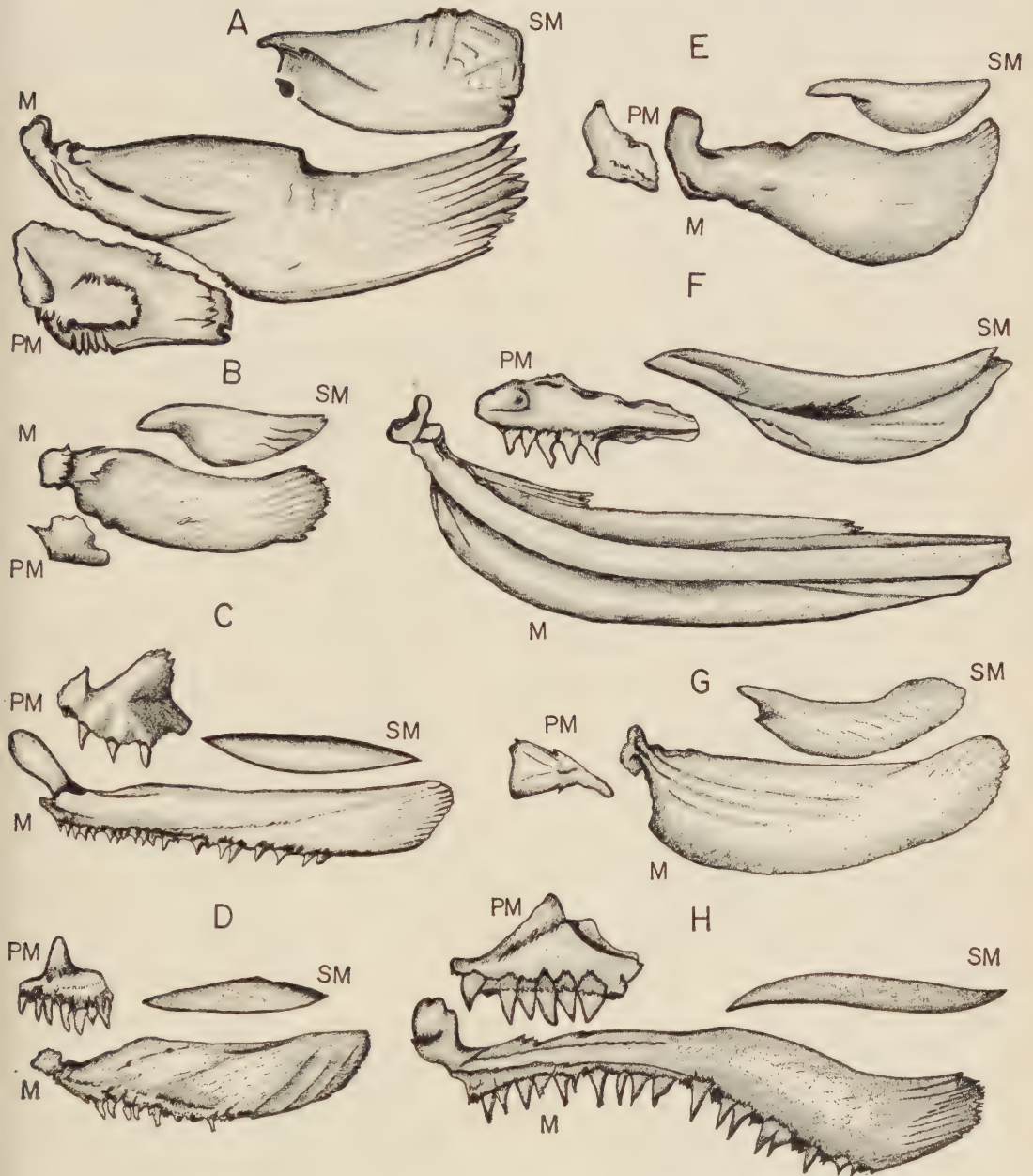
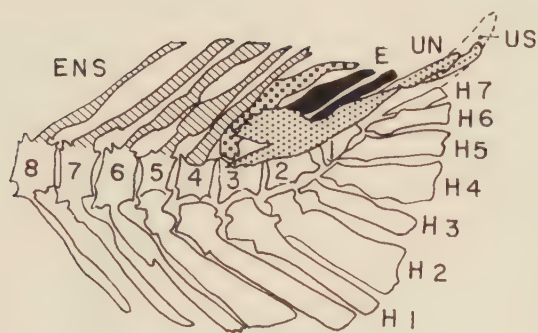


PLATE 14

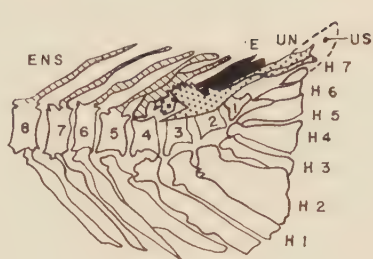
Caudal skeletons of Salmonidae

- A. Type 1, *Salvelinus fontinalis*, UMMZ 69641, about 4.6 ×
- B. Type 2, *Salvelinus namaycush*, UMMZ 162155, about 3.6 ×
- C. Type 3, *Salmo gairdneri*, UMMZ 127601, about 5.1 ×
- D. Type 3, *Salmo trutta*, UMMZ 124553, about 4.1 ×
- E. Type 4, *Salmo trutta*, UMMZ 124553, about 3.6 ×
- F. Type 4, *Salmo salar*, UMMZ 141019, about 4.6 ×
- G. Type 5, *Coregonus artedii*, UMMZ 145300, about 3.1 ×
- H. Type 5, *Prosopium coulteri*, UMMZ 167954, about 3.1 ×

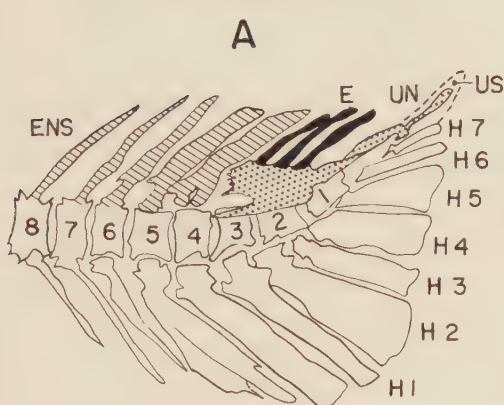
Abbreviations.—E, epural; ENS, expanded neural spine; H, hypural; UN, uroneural; US, urostyle.



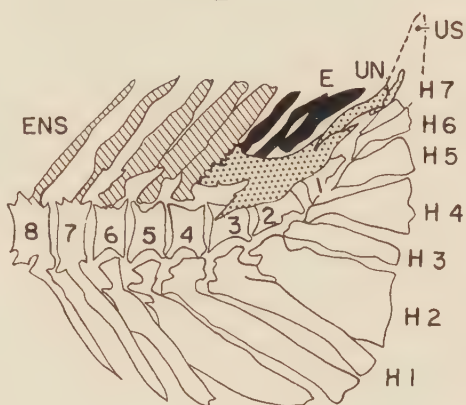
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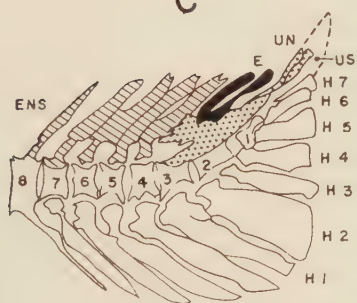
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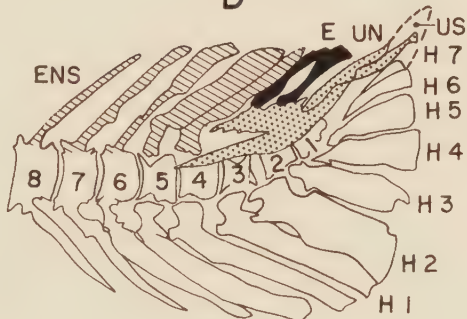
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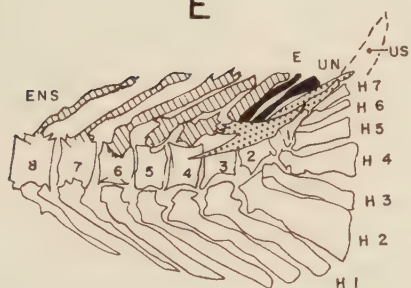
D



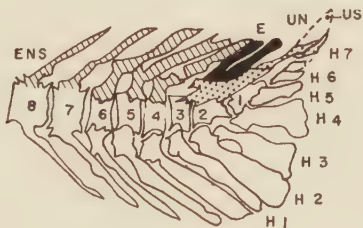
E



F



G



H

PLATE 15

Caudal skeletons of Salmonidae and Elopidae

- A. Type 6, *Oncorhynchus tshawytscha*, UMMZ 146364, about 4.3 ×
- B. Type 5, *Thymallus arcticus*, UMMZ 169574, about 4.9 ×
- C. Type 6, *Hucho perryi*, UMMZ 172490, about 2.4 ×
- D. *Elops affinis*, UMMZ 159257, about 2.8 ×

Abbreviations.—E, epural; ENS, expanded neural spine; H, hypural; UN, uroneural; US, urostyle.

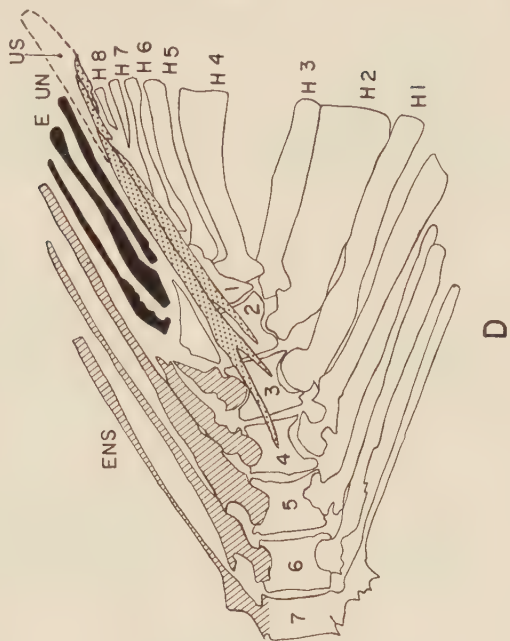
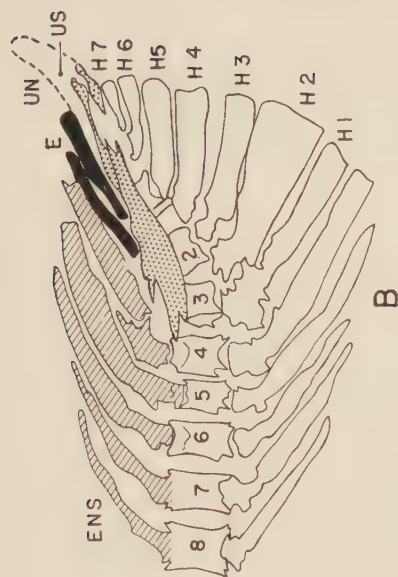
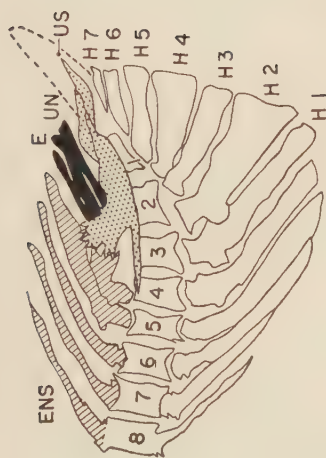
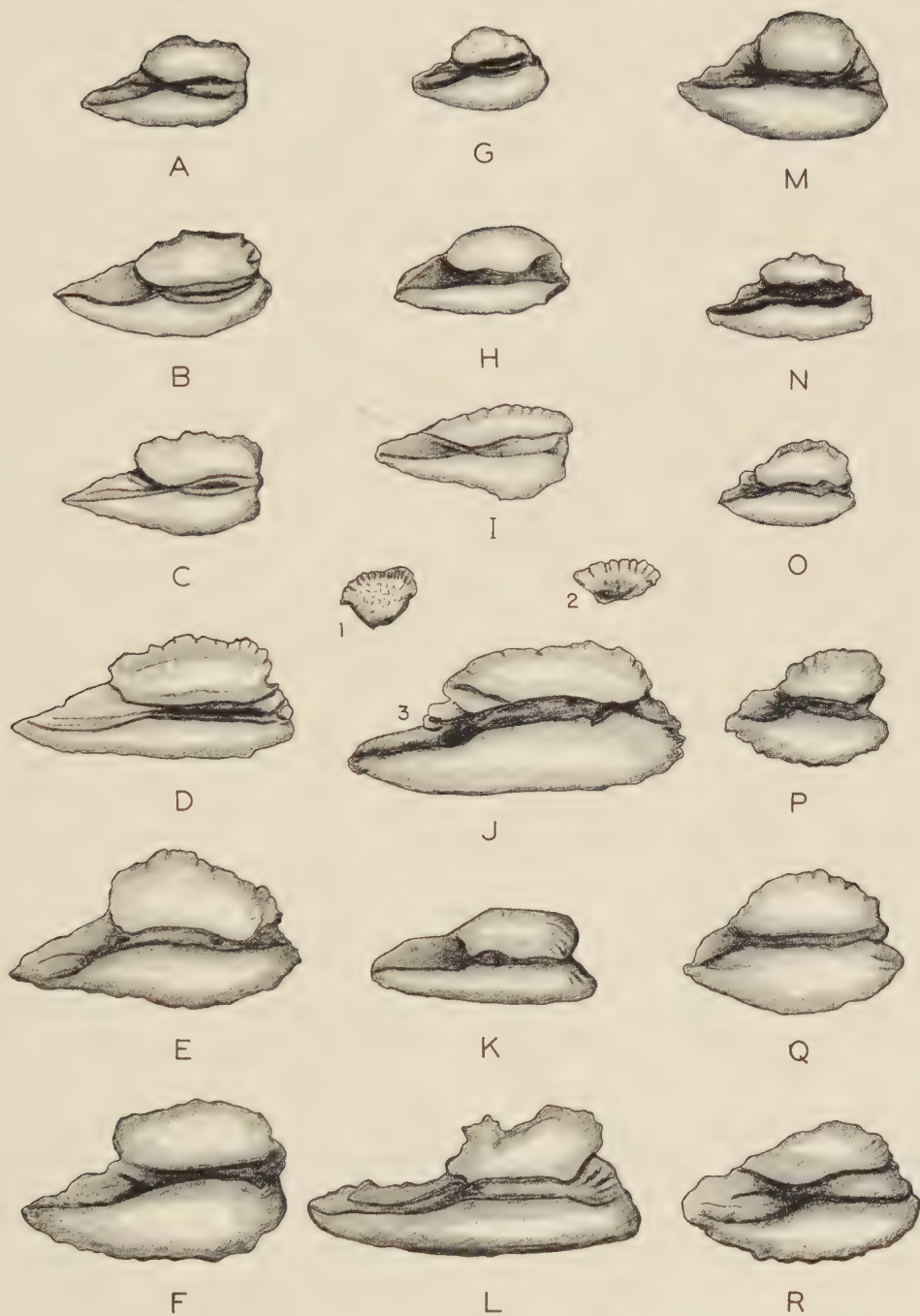


PLATE 16

Otoliths of Salmonidae

- A. *Coregonus kiyi*, UMMZ 172477-S, 1.0 ×
- B. *Coregonus reighardi*, UMMZ 172476-S, 1.6 ×
- C. *Coregonus alpenae*, UMMZ 172475-S, 1.6 ×
- D. *Coregonus artedii*, UMMZ 172467-S, 1.9 =
- E. *Prosopium cylindraceum*, UMMZ 52880, 2.6 ×
- F. *Coregonus hoyi*, UMMZ 172479-S, 2.6 ×
- G. *Salvelinus namaycush*, UMMZ 172463, 1.0 ×
- H. *Prosopium coulteri*, UMMZ 167954, 2.6 ×
- I. *Coregonus clupeaformis*, UMMZ 54314, 1.3 ×
- J. *Thymallus arcticus*, UMMZ 172465-S
 - 1 Lapillus, 2.9 ×
 - 2 Asteriscus, 2.9 ×
 - 3 Sagitta, 2.9 ×
- K. *Prosopium gemmiferum*, UMMZ 141809, 2.6 ×
- L. *Stenodus leucichthys*, UMMZ 172487-S, 1.6 ×
- M. *Salvelinus fontinalis*, UMMZ 172462-S, 2.3 ×
- N. *Salmo trutta*, UMMZ 172470-S, 1.0 ×
- O. *Oncorhynchus keta*, UMMZ 172452-S, 1.6 ×
- P. *Oncorhynchus nerka*, UMMZ 172443-S, 1.6 ×
- Q. *Salmo gairdneri*, UMMZ 172468-S, 2.3 ×
- R. *Oncorhynchus gorbuscha*, UMMZ 172444-S, 2.9 ×



A Systematic Study of the *Salvelinus alpinus* Complex in North America^{1,2}

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ABSTRACT

Sympatric populations of *Salvelinus malma* and *Salvelinus alpinus* from Karluk and Fraser Lakes, Kodiak Island, Alaska, were compared using the discriminant function analysis. The analysis indicated that hybridization between *S. malma* and *S. alpinus* rarely, if ever, occurs in these lakes. Therefore, *S. malma* and *S. alpinus* are considered distinct species. Data on 507 *S. malma* and 411 *S. alpinus* from 77 localities suggest at least two distinct forms of both *S. malma* and *S. alpinus* in North America. Speculations are made on the origin and evolution of *S. malma* and *S. alpinus*.

INTRODUCTION

THE CHARS (*Salvelinus*) form a holarctic genus of salmonid fishes. Morphologically chars are very plastic; stunted populations and colour variants are common. As a result numerous species of *Salvelinus* have been described, many of which are probably synonymous. The present study is an attempt to clarify the systematics of the *Salvelinus alpinus* complex in North America (excluding Greenland). Particular attention is paid to the systematic position of the Dolly Varden, *Salvelinus malma*.

Jordan, Evermann and Clark (1930) list 13 species of *Salvelinus* from North America. These chars fall into three distinct groups: *S. namaycush*, *S. fontinalis*, and the *S. alpinus* group. Most authors now consider each of the first two groups as single species endemic to North America. The third group is circum-polar in distribution, and contains an undetermined number of species. This group is referred to as the Arctic chars, or the "*S. alpinus* complex." Berg (1948) recognizes 11 species of Arctic chars from Russia. Jordan *et al.* (1930) list 4 species of Arctic chars from Greenland and the Canadian arctic. Vladykov (1954) and Walters (1955) suggest the use of the single name *Salvelinus alpinus* for the whole group until more material is available for study.

A char closely related to the *S. alpinus* complex is distributed along the Pacific coasts of North America and Asia. This is the Dolly Varden, *Salvelinus malma* (Walbaum). Several authors (Dymond, 1936, 1947; Carl and Clemens, 1953; Lindsey, 1956) have considered the Dolly Varden a part of the *S. alpinus* complex and refer to it by the subspecific name *Salvelinus alpinus malma*. Other

¹Received for publication January 19, 1961.

²Based on a thesis submitted to the University of British Columbia in partial fulfilment of the requirements for the degree of Master of Science.

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authors (Delacy and Morton 1943, Morton and Miller 1954) consider the Dolly Varden a distinct species, *Salvelinus malma*.

In the following discussion the names *S. alpinus* and *S. malma* are used for the North American species. The author believes these chars are conspecific with the European and Asian chars of the same names. However, no attempt has been made here to equate North American chars with European or Asian species. Where possible, comparisons are made, but due to the inadequacy of published material such comparisons are speculative.

Descriptions of North American *S. malma* and *S. alpinus* are included to facilitate possible future comparisons with European and Asian species. The data on which the following study is based are summarized in an Appendix.

MATERIALS AND METHODS

This study is based on examination of specimens from Washington, British Columbia, Yukon Territory, the Northwest Territories, and Alaska. Material from Alaska, Yukon Territory and northern British Columbia was largely collected during the summers of 1957, 1958 and 1960; *S. alpinus* from the Northwest Territories were principally obtained during the 1959 Barren Grounds Survey of the Arctic Unit of the Fisheries Research Board. The specimens are now in the museums of the Institute of Fisheries of the University of British Columbia, the College of Fisheries of the University of Washington, and the Royal Ontario Museum. Specimens from 77 localities, totalling 507 *S. malma* and 411 *S. alpinus*, were examined. Individuals ranged from 20 to 500 mm in length. Both anadromous and non-migratory populations were sampled.

All meristic counts and measurements follow Hubbs and Lagler (1958). Counts of fin rays, branchiostegal rays and vertebrae were made on cleared specimens under a binocular microscope. Most vertebral counts were made from radiographs. Gill rakers were counted by dissecting out the gill arch and counting the rakers under a binocular microscope. Pyloric caeca were counted as each caecum was detached from the main mass of caeca under a binocular microscope. Gill rakers and pyloric caeca were counted on all specimens examined.

The following measurements were made: fork length, head length, maxillary length, eye diameter, least caudal peduncle depth, and interorbital width.

The numbers of teeth on the tongue and on the basibranchial bones were counted. Tooth counts were made only on cleared and stained specimens. Alveoli from which teeth had been lost were included.

The numbers of spots in the area under the dorsal fin and above the lateral line were counted. Any spots partially in this area were included. Spots were counted only on fish on which the number of spots could be determined accurately. The horizontal diameter of the largest spot touching the lateral line was used as a measure of spot size. Spot size and spot number were found to vary with length and are of little taxonomic value.

The number of gill rakers, the number of pyloric caeca and the pores along the lateral line were found to be the most valuable characters for comparing

S. malma and *S. alpinus*. Vladykov (1954) has criticized the use of gill rakers in char taxonomy. He contends that the number of gill rakers varies with length in char. Correlation coefficients were calculated between length and: number of gill rakers, number of pyloric caeca, and number of pores along the lateral line. In each case, for both species, the correlation was non-significant and quite small (Table I). Therefore, Vladykov's criticism is invalid for these species, and all three characters can be used on specimens within the size range examined.

TABLE I. Correlation (r) of gill rakers, pyloric caeca, and pores along the lateral line with fork length in Karluk Lake *S. malma* and *S. alpinus*, together with the degrees of freedom (d.f.) and probability of significance (P).

	<i>S. malma</i> —33 specimens			<i>S. alpinus</i> —32 specimens		
	r	d.f.	P	r	d.f.	P
Gill rakers lower arch	0.11	31	>0.10	0.26	30	>0.10
Pyloric caeca	0.12	31	>0.10	0.25	30	>0.10
Pores along the lateral line	0.25	31	>0.10	0.24	30	>0.10

TREATMENT OF DATA

All body measurements were plotted against fork length or head length on logarithmic axes (Martin, 1949). These curves showed some differences in the relative growth rates of various body parts for *S. malma* and *S. alpinus*, but none of the differences were sufficient to characterize either species.

Significance of correlations between enumerated characters and length were tested using the correlation coefficient (Snedecor, 1956).

A discriminant function analysis (Fisher, 1936; Rao, 1952) was used on data from two Alaskan collections of char. The computations were done at the University of British Columbia computing centre on an Alwac III computer. Discriminant function analysis is a technique for combining the discriminating power of several characters into a single discriminant score. Hubbs and Kuhne (1937) devised a character index which combined the numerical values of several characters into a single expression. Two major criticisms can be made of the Hubbs character index. Firstly, all of the characters are given equal weight, and secondly, no attempt is made to determine whether the characters combined are correlated. Combining characters into an index without weighting the characters assumes that all of the characters used are of equal value in distinguishing the particular form. This is not always so. Combining correlated characters can produce a biased index. Correlated characters should be combined as a group rather than treated individually.

The discriminant function analysis overcomes both of these objections. Each character is weighted according to the difference between the means of that character for both populations and also for the total variation of the character. The characters that best separate the populations are automatically given the greatest weight. If some of the characters are correlated the best of the correlated

characters is weighted like any other character, and characters correlated with it are given weight only as they contribute to discrimination beyond that provided by their correlate.

This type of analysis requires some preliminary estimate of the differences that exist between the means of the various characters in each of the two populations, necessitating a preliminary division into two groups. The differences thus established are then used to provide statistics for the calculation of a discriminant function that will best combine the various characters to maximize the difference between the two groups. The technique for calculating discriminant scores is given by Rao (1952).

TAXONOMIC RELATIONSHIP OF *SALVELINUS MALMA* AND *SALVELINUS ALPINUS*

To determine whether *S. malma* is a distinct species, or a subspecies of *S. alpinus*, it is necessary to examine samples from areas where the two forms occur together. Several such areas were sampled.

KARLUK LAKE

Karluk Lake is situated on Kodiak Island in the Gulf of Alaska. DeLacy and Morton (1942) reported two closely related species of *Salvelinus* from Karluk Lake. They assigned one species to the *S. alpinus* complex and, because the two forms occur in the same lake, they regarded the other as a distinct species *S. malma*. They presented a morphometric and meristic comparison. Examination of their data reveals no characters that can completely separate the two nominal species in Karluk Lake. All of the characters presented showed some degree of overlap.

If the two forms of chars are distinct species, the overlap in all of the characters examined suggests that introgressive hybridization might occur in Karluk Lake. DeLacy and Morton did not consider hybrids in their discussion.

In June 1958, 65 specimens of *Salvelinus* were collected by the author from Karluk Lake. All collections were made by gill nets or seines. Field observation suggested two types of chars in Karluk Lake. One type was characterized by numerous small, yellowish-red spots, and the other by fewer, larger, bluish-red spots. A few adults and most juveniles could not be distinguished by colour pattern.

The only other character that suggested two populations was the number of gill rakers. The number of gill rakers on the lower limb of the first arch (Fig. 1) has a distinctly bimodal distribution when the entire Karluk Lake sample is plotted. Numbers of males and females are approximately equal in both peaks.

For the preliminary segregation of the sample necessary to provide an estimate of differences in the means the gill raker count was used, for the following reasons. DeLacy and Morton (1942) found that in Karluk Lake the number of gill rakers on the lower limb of the first arch ranged from 8-12 in the *S. malma* form and from 12-15 in the *S. alpinus* form. Also, examination of *S. malma*

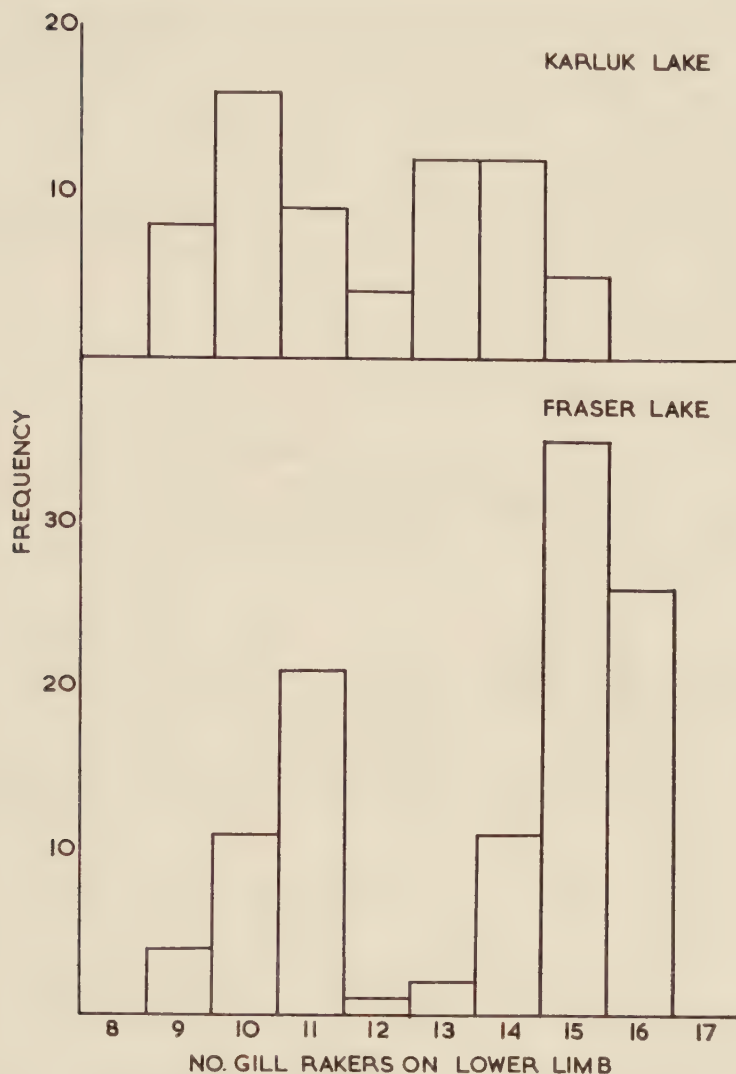


FIG. 1. Distribution of gill rakers on the lower limb of the first arch for the entire Karluk and Fraser Lake samples.

from other nearby areas where only *S. malma* occurs confirmed that the range of gill rakers on the lower limb is from 8–12. Accordingly, the entire Karluk Lake sample was segregated into "*S. malma*"⁴ and "*S. alpinus*" on this basis, with the exception of specimens with 12 gill rakers which were included in both groups. The characters used in the discriminant analysis were: gill rakers, pyloric caeca and pores along the lateral line.

⁴The validity of *S. malma* has not yet been discussed. "*S. malma*" and "*S. alpinus*" are used here for convenience in referring to the two forms of Karluk char.

Figure 2a presents the calculated discriminant scores for the Karluk Lake sample. Two discrete groups are indicated, with a single individual occupying an intermediate position.

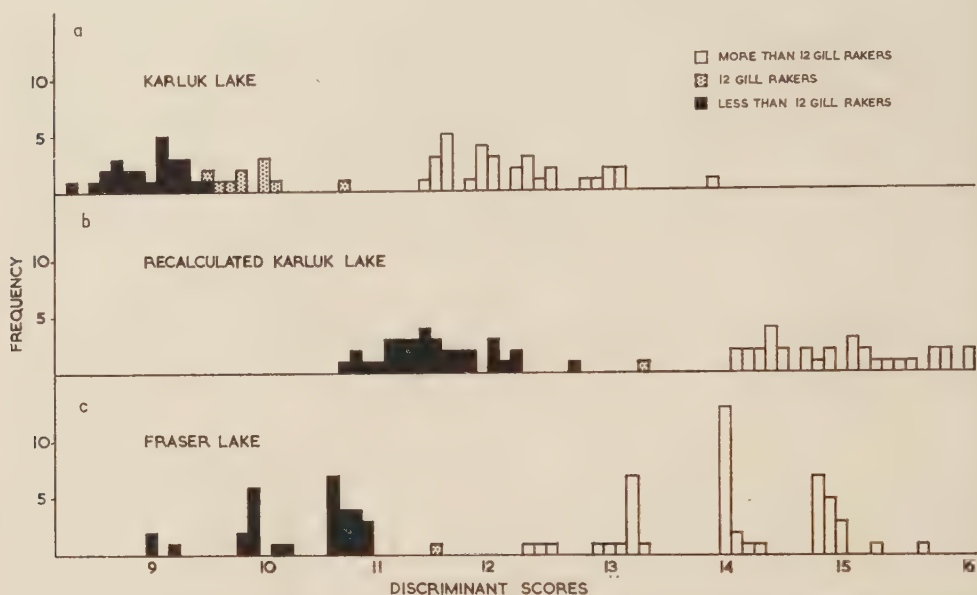


FIG. 2. (a) Distribution of discriminant scores for the Karluk Lake sample. (b) Recalculated Karluk Lake discriminant scores. (c) Distribution of discriminant scores for the Fraser Lake sample.

Eight of the individuals which had intermediate gill raker counts, and which had been included in both groups in the first calculation, can be seen in Fig. 2a to lie within the "*S. malma*" group. Therefore, the eight individuals were reclassified as "*S. malma*" and new discriminant scores were calculated. Figure 2b presents the recalculated discriminant scores for Karluk Lake. The same specimen still occupies an intermediate position.

In spot number and pyloric caeca number the intermediate individual in Fig. 2b is near the mode for "*S. alpinus*" and at the extreme range of Karluk "*S. malma*". DeLacy and Morton⁵ give the range in vertebral counts for Karluk Lake char as 62-66 for "*S. malma*" and 65-69 for "*S. alpinus*"; the vertebral count for this individual is 66. Again the intermediate individual is near the mode for "*S. alpinus*" and at the extreme range of "*S. malma*". These facts suggest that the intermediate is "*S. alpinus*", but do not eliminate the possibility that it is a hybrid.

All of the specimens from Karluk Lake can be separated into two discrete groups, with one possible exception. However, there is still the objection that

⁵DeLacy and Morton (1943) did not include the last two vertebrae in their counts. Two vertebrae have been added to their counts to make them comparable.

differences observed might be phenotypic, a result of the anadromous behaviour of the population of "*S. malma*" in that lake. DeLacy and Morton noted major behaviour differences between the two Karluk Lake forms of *Salvelinus*. The "*S. malma*" form is anadromous while the "*S. alpinus*" form is non-migratory. This difference in environment might account for the morphometric differences between the adult forms in Karluk Lake, which could be anadromous and non-migratory populations of the same species. Fortunately it was possible to test this possibility with samples from a nearby land-locked lake.

FRASER LAKE

Fraser Lake is a short distance east of Karluk Lake on Kodiak Island. It is completely land-locked by a 31-foot (10-metre) falls on the outlet stream.

In June, 1958, 92 specimens of *Salvelinus* were collected in Fraser Lake by gill nets and seine. As in Karluk Lake, gill raker number was the only character to show bimodality when the frequency distributions of the entire sample were plotted. For reasons discussed previously, the sample was segregated into "*S. malma*" and "*S. alpinus*" on the basis of the number of gill rakers on the lower limb of the first arch. The discriminating powers of the same four characters were again combined into a discriminant score. On this basis the specimens from Fraser Lake can be separated into two discrete groups (Fig. 2c). One individual has a somewhat intermediate score, but is much closer to the "*S. malma*" group than to the "*S. alpinus*" group. In spot number and spot size this individual lies within the range of both "*S. malma*" and "*S. alpinus*", but in both of these characters it is near the mean of the "*S. malma*" group and at the extreme range of the "*S. alpinus*" group. The vertebral count for this fish is 64, which is outside of the range for *S. alpinus* in Karluk Lake. These facts suggest that the intermediate is "*S. malma*".

KENAI RIVER

Two specimens were collected from Kenai River on the Kenai Peninsula, Gulf of Alaska. One char had 12 gill rakers on the lower limb of the first arch, 27 pyloric caeca and numerous small spots. The other char had 13 gill rakers on the lower limb, 32 pyloric caeca and fewer, larger spots. These two Kenai fishes probably represent "*S. malma*" and "*S. alpinus*" respectively.

LAKE ALEKNAGIK AND TRIBUTARIES

Lake Aleknagik is the first in a series of lakes at the headwaters of the Woods River, which enters Bristol Bay near Dillingham, Alaska. Samples were obtained from the lake and from Hansen Creek, a small tributary entering the east side about 3 miles north of the lake outlet.

Table II presents a comparison of adult char collected in Lake Aleknagik and in Hansen Creek. Judging from the Karluk and Fraser Lakes samples the number of gill rakers on the lower limb of the first arch is the best morphological difference between "*S. malma*" and "*S. alpinus*". The mean number of gill rakers

TABLE II. Comparison of chars from Lake Aleknagik and Hansen Creek (based on 30 specimens from each locality).

	Lake Aleknagik		Hansen Creek	
	Range	Mean	Range	Mean
Gill rakers lower limb	12-17	15.1	11-14	12.9
Pyloric caeca	29-74	52.5	21-30	26.7
Vertebrae	66-71	67.6	66-70	67.6

on the lower limb in the Lake Aleknagik sample is 15.1, with a range of 12-17. This, and all other characters examined, indicate that the Lake Aleknagik sample represents "*S. alpinus*".

The Hansen Creek sample is less easy to classify. Table I shows that, by Karluk and Fraser Lake standards, the Hansen Creek fish resemble "*S. alpinus*" in vertebral count, resemble "*S. malma*" in caecal count, and are intermediate in gill raker number. The spot pattern of the Hansen Creek fish suggests "*S. malma*", but the fish are small and spot size and number are correlated with length. The Hansen Creek sample is therefore intermediate between "*S. malma*" and "*S. alpinus*" in gill raker number, but like "*S. alpinus*" in number of vertebrae, and like "*S. malma*" in number of pyloric caeca.

There are several possible explanations for the Hansen Creek chars. They may be a dwarf, stream-dwelling population of the "*S. alpinus*" which occur in Lake Aleknagik. In this case the unusual number of gill rakers and pyloric caeca might be the result of the stream environment. However, dwarf, stream-dwelling *S. alpinus* from Baffin Island have the same number of gill rakers and pyloric caeca as normal *S. alpinus* from the same area (Table III). This suggests

TABLE III. Comparison of dwarf and normal *S. alpinus* from Baffin Island (10 specimens from each locality).

	Dwarf chars Sapuladjuk		Normal chars Nettilling Lake	
	Range	Mean	Range	Mean
Gill rakers lower limb	14-17	16	14-17	16
Pyloric caeca	32-47	38	29-46	38

that the unusual meristic counts of the Hansen Creek chars are not the result of environment. The Hansen Creek chars probably represent a genetically distinct form of *Salvelinus*.

Another possible explanation of the Hansen Creek chars is that they are the result of hybridization between "*S. malma*" and "*S. alpinus*". Hubbs (1955) suggests that interspecific hybrids in fishes are usually intermediate in all characters in which those species differ. The Hansen Creek chars are intermediate in the number of gill rakers, but not in other meristic characters. Ecologically the Hansen Creek chars appear to be closer to "*S. malma*" than to "*S. alpinus*". They are not known to occur in the lake, and apparently spawn in the stream.

The present author considers the Hansen Creek chars a form of "*S. malma*". The problem is discussed further in the section on the validity of subspecies in *S. malma*.

BROOKS LAKE AND TRIBUTARIES

Brooks Lake is located on the Alaska Peninsula and drains into Bristol Bay by the Naknek River. In 1958 a sample of 21 char was collected from Brooks Lake and its tributaries by Mr T. Merrill of the United States Fish and Wildlife Service. Twenty of the char were from tributaries and one from Brooks Lake proper.

The single specimen from Brooks Lake has 14 gill rakers on the lower limb of the first arch, 43 pyloric caeca, and is undoubtedly "*S. alpinus*". The 20 fish from tributary streams have a mean of 12.6 gill rakers on the lower limb, with a range of 11–14. In this character they are intermediate between "*S. malma*" and "*S. alpinus*". The vertebral count of the sample from the tributaries ranges from 67–69 with a mean of 68, and in this character it resembles "*S. alpinus*". The number of pyloric caeca for the tributary sample ranges from 21–36 with a mean of 27.9. In this character the tributary sample resembles "*S. malma*".

The sample from tributaries to Brooks Lake is very similar morphologically to the Hansen Creek sample and presents the same problem.

SALMON LAKE AND TRIBUTARIES

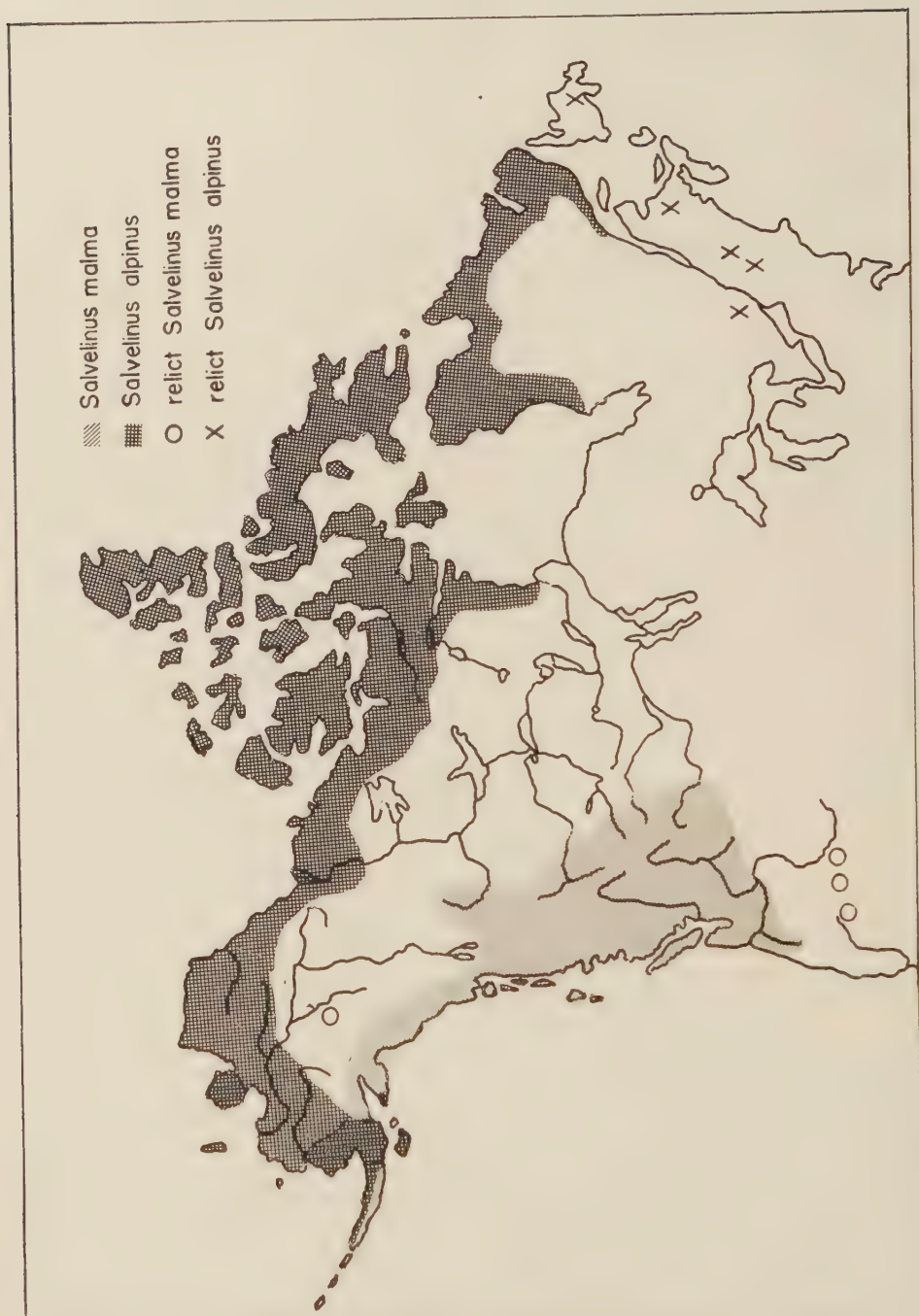
Salmon Lake is located on the Seward Peninsula and drains into the Bering Sea by the Pilgrim River. A sample of 31 chars was obtained from Salmon Lake and a clear tributary stream. One char was from the lake proper, and 30 were from the tributary stream.

The single char from Salmon Lake has 15 gill rakers on the lower limb of the first arch, and represents "*S. alpinus*". The sample from the tributary stream has a mean of 12.8 gill rakers on the lower limb, with a range of 11–14. The number of vertebrae range from 65–71, with a mean of 67.8. The number of pyloric caeca range from 24–31, with a mean of 28.

In all of the characters examined the chars from the tributary to Salmon Lake are similar to the chars from tributaries to Aleknagik and Brooks Lakes. They are considered to be the same form.

SUMMARY OF THE TAXONOMIC RELATIONSHIP OF "*S. malma*" AND "*S. alpinus*"

The validity of doubtful species pairs can be established if they occur sympatrically without mass hybridization. Occasional hybridization may occur, but as long as the hybrids are rare the species can be considered valid. In Karluk and Fraser Lakes *S. malma* and *S. alpinus* occur sympatrically. The evidence indicates that within these lakes hybridization between *S. malma* and *S. alpinus* rarely, if ever, occurs. The two specimens from Kenai River also appear to represent these two species. North of the Alaska Peninsula the distinction is not so clear, but in two Bristol Bay localities and one on the Seward

FIG. 3. North American distribution of *S. malma* and *S. alpinus*.

Peninsula a common pattern is evident. In lakes, a type of fish occurs which agrees closely with *S. alpinus* of the Gulf of Alaska area, while in streams there occurs a smaller form which is distinct from *S. malma* south of the Alaska Peninsula. This stream-dwelling form is here regarded as a northern form of *S. malma*.

From the data presented, *S. alpinus* and *S. malma* are considered as discrete species, each subject to geographic variation, which occur sympatrically in certain areas of Alaska (Fig. 3) with little or no hybridization.

In the following sections each species will be treated separately. The species will be described, its distribution discussed, and the validity of its subspecies examined.

DESCRIPTION OF *SALVELINUS MALMA*

The following description includes data from the entire North American range of *S. malma*. Where there are distinct forms of *S. malma* the differences between these forms are noted.

Head 3.2 to 5.8 into fork length (Fig. 4). D. 13-16 (all rays); A. 11-15 (all rays). Body elongate, somewhat rounded; vertical eye diameter 4-5.5 into head; mouth terminal, large; maxillary usually reaching to a point behind posterior margin of the eye. In dwarf stream-dwelling forms the maxillary often does not reach beyond the posterior margin of the eye. Teeth

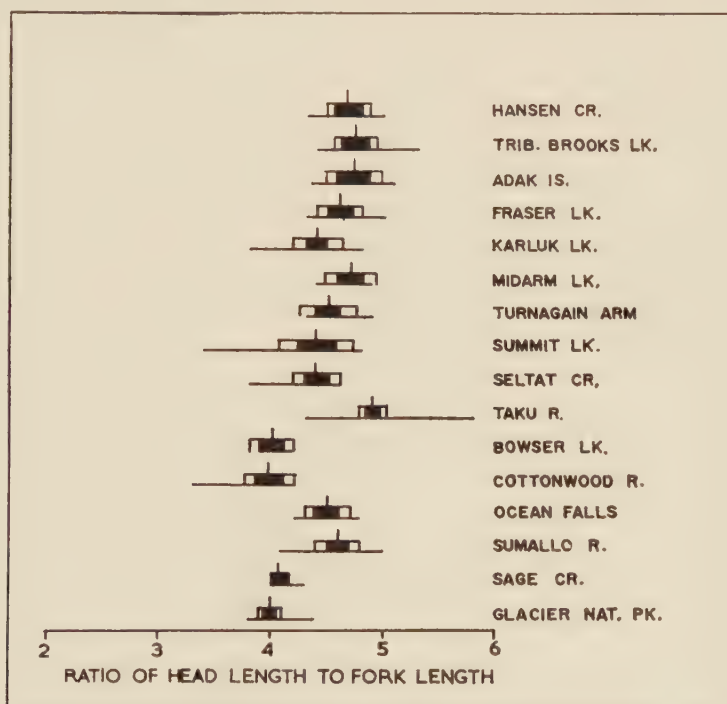


FIG. 4. Geographic variation in the ratio of head length to fork length for North American *S. malma*.

on head of vomer only, palatine teeth and vomerine teeth sometimes continuous, usually not; 7-15 teeth on tongue; 0-44 teeth on the basibranchial bones, the number of teeth on the basibranchial bones increases with length. Gill rakers on first arch 11-26; gill rakers on lower limb of first arch 8-14 (11-14 in the northern form, 8-12 in the other forms); gill rakers on upper limb of first arch 3-9. Pyloric caeca 13-47 (19-47 in the northern and southern forms, 13-18 in the central Alaska form). Branchiostegal rays 21-30, usually more on left side than on right side. Total number of vertebrae 57-70 (65-71 in the northern form, 57-66 in the other forms). Lateral line slightly decurved anteriorly, then straight, often with a dip or arch posteriorly; pores along the lateral line 105-142.

Colour variable; blue, olive-green or brown on dorsal surface; occasionally bright red on sides, sea-run individuals silvery. Pelvic and anal fins often with creamy leading edges. Some individuals with a distinct dark streak along the inner edge of the dentary. Yellow, orange or red spots on dorsal surface and sides; spots round, small and numerous, the largest touching lateral line 3-7 times into interorbital width. Dorsal surface occasionally with vermiculations. Juveniles and dwarf adults with 8-10 wide parr marks.

DISTRIBUTION

Salvelinus malma ranges from northern California around the rim of the North Pacific and Bering Sea to Japan and Korea (Fig. 3). Over most of this range *S. malma* has both anadromous and non-migratory populations. At the southern extremes of its range *S. malma* is usually non-migratory. Taranetz (1936) reports anadromous populations of *S. malma* as far south as Peter the Great Bay. Non-migratory forms are found in southern Honshu and in the Yalu River (Taranetz, 1936). In North America (Fig. 5) the southern extent of the range is represented by isolated, non-migratory populations in northern Nevada (Miller and Morton, 1952) and northern California (Wales, 1957).

In Asia *S. malma* is reported north to the Anadyr River (Berg, 1948). The exact northern limits of the range in North America are unknown. *Salvelinus malma* has been reported from Point Hope and Herschel Island (Scofield, 1899), and from the Colville River mouth, Pergniak and Point Barrow on the arctic slope of Alaska (Murdoch, 1885). However, *S. alpinus* is common in these areas, and some records of *S. malma* may be due to confusing the two species. Figure 3 gives the northern range of *S. malma* in North America based on specimens examined by the author.

S. malma is not common in central Alaska and central Yukon Territory, where it appears to be confined to head-water habitats. Evermann and Goldsborough (1907) report *S. malma* from Mynock Creek (tributary to the Yukon River) near Rampart. The only *S. malma* obtained by the present author from central Alaska were from Dry Creek, a small tributary of the Tanana River. No *S. malma* were taken in the Tanana or Yukon Rivers proper. Wynne-Edwards (1947) reports *S. malma* from the clear streams of the Mackenzie and Richardson Mountains. *Salvelinus alpinus* occurs in the Richardson Mountains, and probably also in the Mackenzie Mountains. Lacking actual specimens, Wynne-Edwards' records of *S. malma* from these areas could be due to confusing *S. malma* with *S. alpinus*. Preble (1908) reports *S. malma* from the headwaters of the Peel River. Some of the headwaters of the Peel rise in the Mackenzie Mountains, and Preble's record also should be treated with reservation. *S. malma*

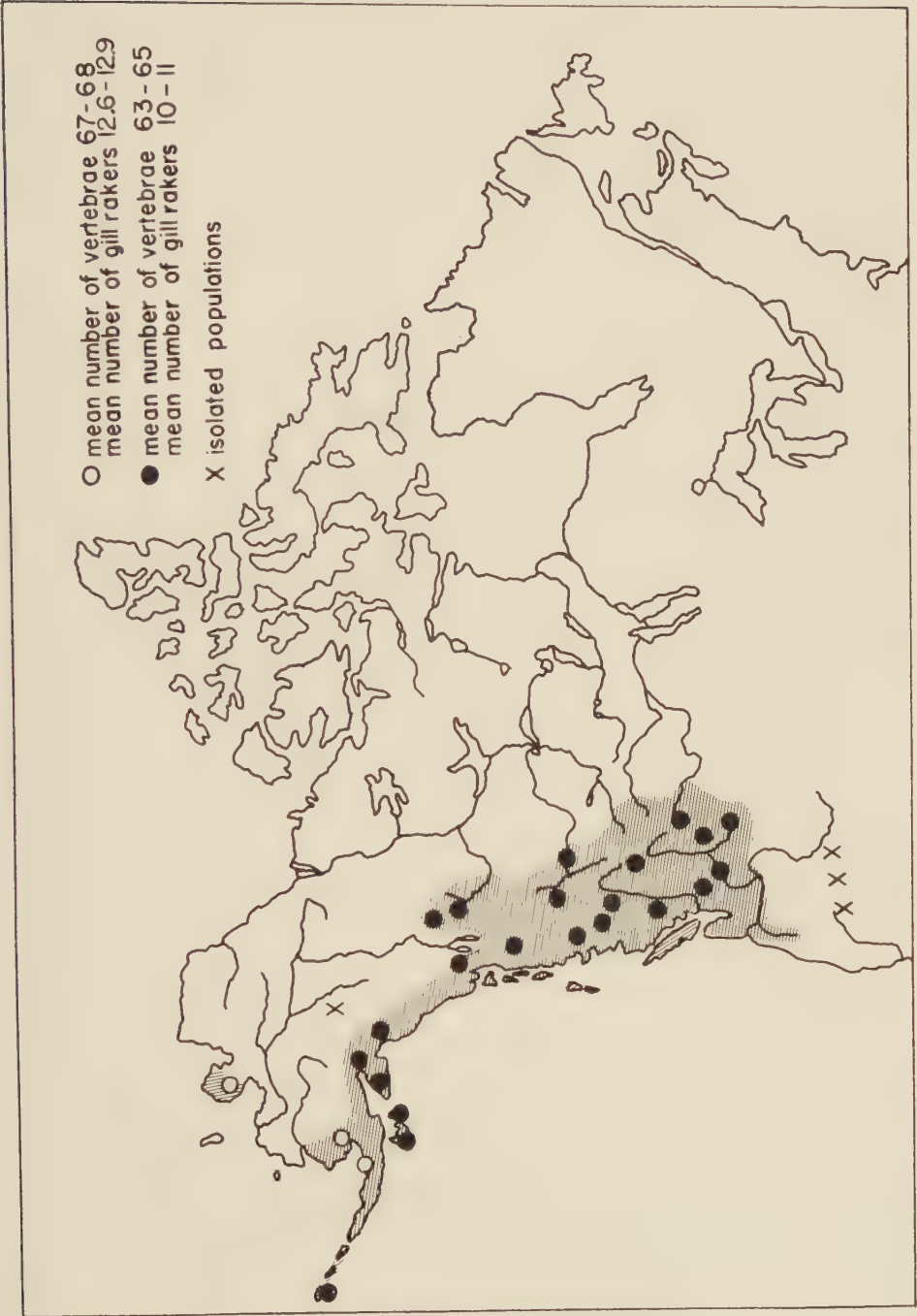


FIG. 5. Geographic variation in the number of vertebrae and gill rakers in North American *S. malma*.

is widely distributed in the upper Liard River (Mackenzie system), and in the Swift River, a small headwater of the Yukon River.

In British Columbia *S. malma* is widely distributed in all river systems except the Okanagan (Carl and Clemens, 1953). On the east slope of the Rocky Mountains *S. malma* is abundant in the headwaters of the South Saskatchewan, North Saskatchewan, Athabaska and Peace Rivers but does not extend far onto the plains. *S. malma* is widely distributed throughout most of the Columbia River system, but has only been reported once (Hubbs and Miller, 1948) from the Snake River above Shoshone Falls.

VALIDITY OF SUBSPECIES

Salvelinus malma was originally described from the rivers of Kamchatka (Walbaum, 1792). Recent Russian authors (Taranetz 1933, 1936; Berg, 1948) recognize two subspecies⁶, *S. m. malma* and *S. m. krasheninnikovi* Taranetz from the Pacific coast of Asia. *S. m. malma* is distributed north of the Gulf of Amur, while *S. m. krasheninnikovi* is distributed south of the Gulf of Amur. *S. m. krasheninnikovi* is distinguished from *S. m. malma* by the number of vertebrae and the number of pores along the lateral line (59–64 vertebrae and 115–133 pores in *krasheninnikovi*, 64–69 vertebrae and 132–140 pores in *malma*).

In North America there are also two distinct forms of *S. malma*. The form found north of the Alaska Peninsula has 65–71 vertebrae and 11–14 gill rakers on the lower limb of the first arch. The *S. malma* occurring south of the Alaska Peninsula and in the Aleutian Islands have 57–67 vertebrae and 8–12 gill rakers on the lower limb of the first arch. There is no evidence of a broad cline between these two forms (Fig. 5).

The northern and southern forms of *S. malma* probably originated from a single population which was divided by glaciation. The northern form evolved in the unglaciated coastal areas of Alaska and Siberia. In North America the southern form evolved to the south of the ice sheet.

In number of vertebrae the two North American forms are in close agreement with the Russian subspecies. However, the exact relationship between the North American and Asiatic forms can not be determined until more information becomes available. Until such a time it is convenient simply to refer to the North American forms of *S. malma* as either northern or southern.

Four specimens of *S. malma* were obtained from Dry Creek near Fairbanks in the unglaciated portion of central Alaska. Comparison of the Dry Creek Dolly Varden with other populations revealed a major morphological difference. The Dry Creek specimens had a very low number of pyloric caeca, ranging from 13 to 18 with a mean of 16. In normal populations the number of pyloric caeca ranges from 19 to 47 with a mean of 26 to 28. The Dry Creek population probably represents a distinct form of *S. malma* which has been isolated in central Alaska since before the last glaciation. Whether the central Alaska Dolly Varden

⁶Taranetz (1936) lists two infraspecies from Russia, *Salvelinus malma* infraspecies *curilus* (Pallas) and *Salvelinus malma* infraspecies *kuznetzovi* Taranetz. These forms are apparently ecotypes.

warrant subspecific designation cannot be determined until more specimens become available.

Jordan *et al.* (1930) suggest that in North America *S. malma* intergrades southwards to form the subspecies *Salvelinus malma spectabilis*. *S. m. malma* is said to be distinguished from *S. m. spectabilis* by the length of the head (less than $\frac{1}{4}$ into standard length in *S. m. malma*, more than $\frac{1}{4}$ in *S. m. spectabilis*). Figure 4 indicates that there is some geographic variability in the length of the head relative to body length, but no evidence to support subspecific distinction based on this character.

Jordan *et al.* (1930) list the Japanese *Salvelinus pluvius* (Hilgendorf) as a synonym of *S. malma*. Recent Japanese authors (Aoyagi, 1957; Matsubara, 1955; Okado, 1955) consider *S. pluvius* to be a distinct species. Aoyagi (1957) distinguishes *S. malma* from *S. pluvius* on the basis of gill rakers and parr marks (16-26 gill rakers and no parr marks in adult *S. malma*, 11-20 gill rakers and parr marks in adult *S. pluvius*). The gill raker count for *S. pluvius* is based on 7 specimens. Even with this small number the gill raker count considerably overlaps that given for *S. malma*. In North America stunted populations of *S. malma* commonly have parr marks as adults. Aoyagi (1957) reports *S. malma* from Hokkaido and *S. pluvius* from Honshu; presumably their ranges never overlap. The evidence suggests *S. pluvius* is a geographic form of *S. malma* and probably should not be considered a distinct species. Whether *S. pluvius* should be considered a separate subspecies of *S. malma* cannot be determined from the available evidence.

Bailey *et al.* (1954) suggest that "a species is properly divisible into subspecies when data have been suitably published to demonstrate that it consists of two or more allopatric populations, each displaying a high degree of uniformity over its range and differing with a high constancy (a figure of at least 93 per cent of individuals is suggested) from other forms, each of which intergrades over a relatively narrow geographic area with at least one other form". In North America there are at least two allopatric forms of *S. malma* which probably fulfill the above criteria. However, in order to avoid synonymies these forms should not be given subspecific designation until their relationship to Asiatic subspecies can be determined.

DESCRIPTION OF *SALVELINUS ALPINUS*

The following description includes data from the entire North American range of *S. alpinus*. Where there are distinct forms of *S. alpinus* the differences between these forms are noted.

Head 3.6-4.8 into fork length. D. 12-16 (all rays); A. 11-15 (all rays). Body elongate, somewhat rounded; vertical eye diameter 3.8-5.4 into head; mouth terminal, large; maxillary usually reaching past posterior margin of the eye. In non-migratory populations the maxillary often does not reach beyond the posterior margin of the eye. Teeth on head of vomer only; spacing between the palatine and vomerine teeth variable; 10-24 teeth on tongue; 20-85 teeth on the basibranchial bones (the number of teeth on the basibranchial bones is extremely variable within populations). Gill rakers on lower limb of first arch 12-19 (mean in the lower Yukon

area approximately 13.5, mean over the rest of the North American range approximately 16); gill rakers on upper limb of first arch 7-13. Pyloric caeca 20-74 (mean in lower Yukon area approximately 29, mean over the rest of the North American range is usually near 44). Total number of vertebrae 60-71. Lateral line slightly decurved anteriorly, then straight, often with a dip or arch posteriorly; pores along the lateral line 123-152.

Colour variable; blue, olive green or brown on dorsal surface; sides often bright orange or red, sea-run individuals silvery. Pelvic and anal fins often with creamy leading edges. Usually a distinct dark streak along the inner edge of the dentary. Pale pink to red spots on dorsal surface and sides (some individuals without spots); spots round, those along the lateral line are usually semi-circular; spots less numerous than in *S. malma* and usually larger, 1.8-6 times into inter-orbital width. In the Bering Sea region the spots above the lateral line often have a narrow blue halo. Juveniles and dwarf adults with 8-15 wide parr marks.

DISTRIBUTION IN NORTH AMERICA

S. alpinus is circumpolar in distribution. In North America it ranges from Alaska along the Arctic coast to the New England states (Fig. 6). Over most of this range *S. alpinus* has both anadromous and non-migratory populations, but at the southern extremes of its range it is usually non-migratory. In North America the southern limit is represented by non-migratory populations on Kodiak Island in the west and by isolated, non-migratory populations in Quebec, Newfoundland, New Brunswick, New Hampshire and Maine in the east. *S. alpinus* extends northward to the limit of land.

In Hudson Bay *S. alpinus* is distributed south to the Churchill River (Vladykov, 1933) on the west coast of the bay, and to Cape Jones on the east coast (Halkett, 1919).

In the Northwest Territories *S. alpinus* is widely distributed along the sea coast. Anadromous *S. alpinus* ascend most of the rivers. *S. alpinus* ascends the Thelon River as far as Beverly Lake, and is distributed throughout the Back River system. *S. alpinus* ascends the Mackenzie River as far as Ft. Good Hope (Wynn-Edwards, 1947). Wynn-Edwards also reports chars from the Mackenzie and Richardson Mountains; it is not known whether these are *S. malma* or *S. alpinus*.

S. alpinus is widely distributed along the Arctic and Bering Sea coasts of Alaska. Anadromous populations ascend most rivers. Walters (1955) reports *alpinus*-like chars from the headwaters of the Colville, Hulahula and Yukon Rivers. The species of these chars is not known. In the lower Yukon and Kuskokwim area *S. alpinus* is found mainly in clear lakes and streams.

VALIDITY OF SUBSPECIES

Salvelinus alpinus was originally described from Scandinavia. At present the taxonomy of the European chars is confused. As a result it is not possible to determine the relationship of North American to European *S. alpinus*.

The following species of Arctic chars have been described from the eastern Canadian arctic; *Salvelinus rossii* (Richardson), *Salvelinus alipes* (Richardson), *Salvelinus nitidus* (Richardson), *Salvelinus arcturus* (Günther) and *Salvelinus*

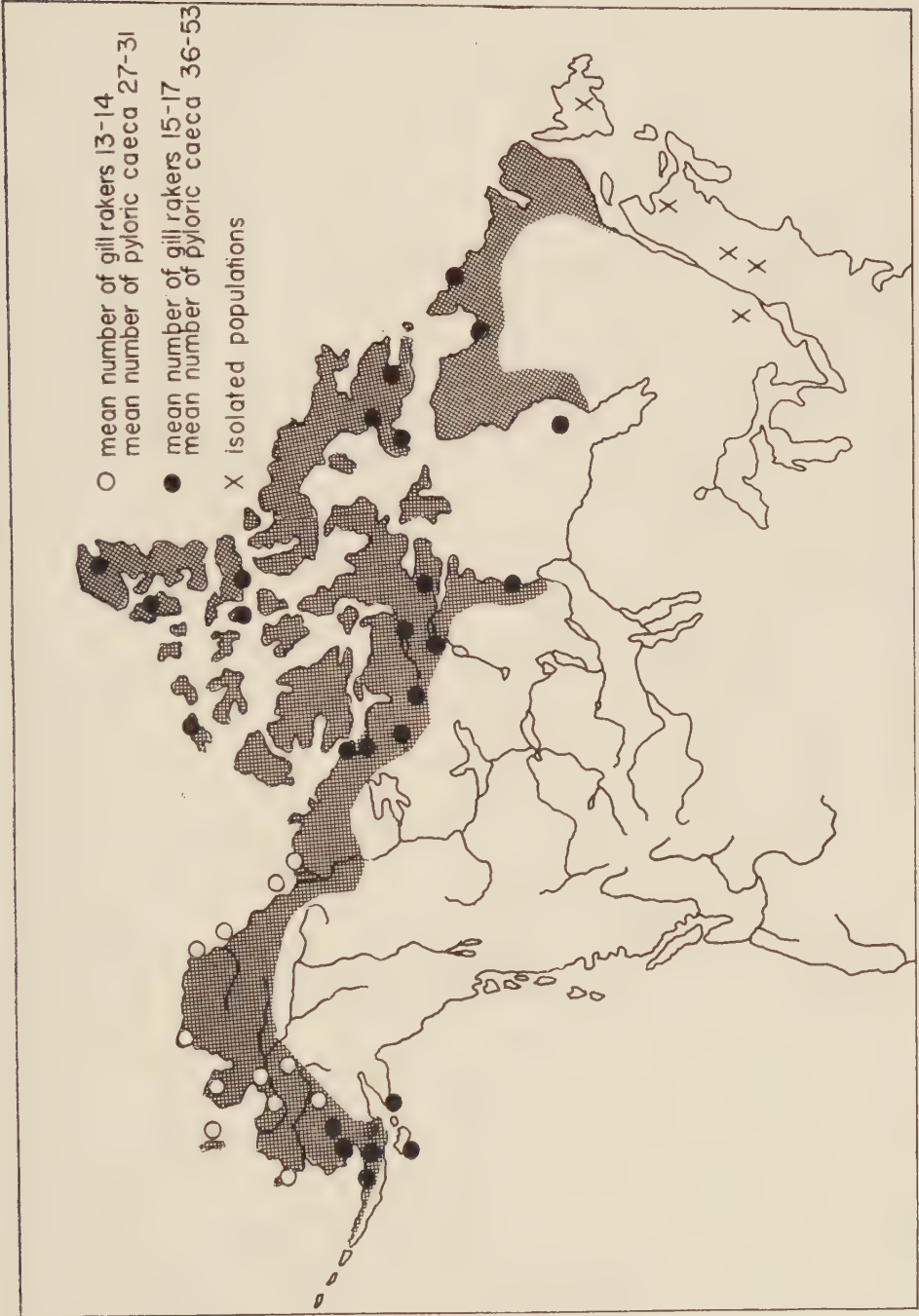


FIG. 6. Geographic variation in the number of gill rakers and pyloric caeca in North American *S. alpinus*.

naresii (Günther). These species were based on small samples and were inadequately described. Where the descriptions mention gill rakers, pyloric caeca or vertebrae the number is always within the range for *S. alpinus*. Examination of anadromous and non-migratory chars from Alaska, Northwest Territories and Labrador revealed no evidence to support the division of the North American Arctic chars into several species.

S. alpinus is represented in Quebec, New Brunswick, Newfoundland, New Hampshire and Maine by isolated, non-migratory populations. These populations were originally given specific designation: *S. marstoni* (Garman) in Quebec, *S. aureolus* (Bean) in New Hampshire and Maine, and *S. oquassa* (Girard) in western Maine. Backus (1957) considers these forms glacial relicts of *S. alpinus*. Vladykov (1954) suggests that *S. marstoni* and *S. oquassa* may be the same species, but that *S. aureolus* is a distinct species. Vladykov (1957) has divided *S. marstoni* into three subspecies: *S. marstoni marstoni*, *S. marstoni intermedius* and *S. marstoni cavanaghi*. These subspecies are largely based on characters that Vladykov (1954) dismissed as being useless in char taxonomy.

In number of gill rakers, pyloric caeca and vertebrae *S. marstoni*, *S. aureolus* and *S. oquassa* are all within the range of variation for North American *S. alpinus*. Vladykov (1954) has suggested that the details of the caudal skeleton are useful in distinguishing *S. alpinus*, *S. marstoni* and *S. aureolus*. Examination of radiographs of 70 specimens of *S. alpinus* and *S. malma* reveal that the range of variation in the details of the caudal skeleton is very wide. Such characters are evidently of little value in distinguishing closely related species of chars. For these reasons *S. marstoni*, *S. aureolus* and *S. oquassa* are considered synonyms of *S. alpinus*. Whether these forms warrant subspecific status can not be determined on the available evidence.

In western North America there are two distinct forms of *S. alpinus* (Fig. 6). The *S. alpinus* distributed from the lower Kuskokwim to the Mackenzie River have 20–36 pyloric caeca (with a mean of approximately 29) and 12–15 gill rakers on the lower limb of the first arch (with a mean of approximately 13.5). The *S. alpinus* distributed east of the Mackenzie River, and those south of the Kuskokwim, have 25–74 pyloric caeca (with a mean of approximately 44) and 12–17 gill rakers on the lower limb of the first arch (with a mean of approximately 16).

Figure 6 suggests that the eastern form of *S. alpinus* (black dots) was once continuously distributed across the North American arctic. It is suggested that this continuous distribution was interrupted by a glaciation (perhaps the Wisconsin). Populations of this form probably survived in the Bristol Bay area, and perhaps on Kodiak Island, as well as south of the ice sheet in eastern North America. The form represented by the white dots in Fig. 6 probably evolved along the arctic slope of Alaska and Siberia. The forms were geographically isolated by the Bering land-bridge in the west and the Continental ice-sheet in the east. The present distribution of both forms has probably been attained by post-glacial dispersal from the above mentioned areas.

These forms of *S. alpinus* may warrant subspecific designation. However, this should be avoided until the relationship between the Eurasian and North American forms of *S. alpinus* can be determined.

ORIGIN AND DISPERSION OF *S. MALMA* AND *S. ALPINUS*

The morphological similarity between *S. malma* and *S. alpinus* suggests that they are derived from a common ancestor. Some speculation can be made concerning the time at which *S. malma* and *S. alpinus* diverged.

Ekman (1953) presents evidence indicating a fairly comprehensive faunistic connection between the cold-temperate faunas of the Atlantic and Pacific during the late Pliocene or early Pleistocene. If *S. malma* had been differentiated at this time it is likely that it would have reached the North Atlantic. Relict populations of *S. malma* in unglaciated parts of Alaska, northern California, Japan and Korea indicate that *S. malma* was widely distributed in the North Pacific area prior to the last Pleistocene glaciation. Relict populations of *S. alpinus* in Quebec, New Brunswick, Newfoundland, New Hampshire, Maine and Europe indicate that *S. alpinus* was widely distributed in the North Atlantic area prior to the last Pleistocene glaciation. *S. malma* and *S. alpinus* must, therefore, have diverged sometime in the Pleistocene prior to the last glaciation.

Before the first Pleistocene emergence of the Bering land-bridge the ancestor of *S. malma* and *S. alpinus* was probably distributed continuously from the North Pacific to the North Atlantic. During the Pleistocene the North Pacific was separated from the Arctic Ocean several times by the land-bridge. During one of these periods of isolation *S. malma* probably evolved to the south of the land-bridge and *S. alpinus* to the north. It is generally accepted that the land-bridge was flooded during the interglacial periods, although Ekman (1953) indicates that very little is known about possible interglacial communications between the North Pacific and North Atlantic. *S. malma* must have evolved prior to one of these interglacial floodings, but did not extend itself into the Atlantic. Neave (1958) suggests that throughout the available interglacial intervals the physical conditions of the Polar Sea did not become much more favourable than they are at present. The present range of *S. malma* does not extend far, if at all, into the Arctic Ocean. It may be supposed that there is some physical factor limiting the northward distribution of *S. malma* and that this prevented the spread of *S. malma* into the Arctic Ocean during the interglacial periods. *S. alpinus* probably reinvaded the North Pacific during each interglacial period.

Morphologically *S. malma* and *S. alpinus* are very similar. Both species spawn in the fall or early winter. Evidence from related species (Stenton, 1952; Buss and Wright, 1956) suggest that the interbreeding of *S. malma* and *S. alpinus* would produce fertile offspring. Therefore, some mechanism for preventing hybridization must have evolved while *S. malma* and *S. alpinus* were geographically isolated. It is suggested that the incipient species developed differences in spawning behaviour which prevented interbreeding after the geographical barriers separating them were broken down. This suggestion is

supported by the spawning behaviour of the two species in Karluk Lake. In the Karluk system *S. malma* spawns in tributary streams, and *S. alpinus* spawns in lakes (DeLacy and Morton, 1942). This behavioural difference, where absolute, could provide a mechanism which prevents formation of hybrids.

In North America *S. malma* probably survived the last Pleistocene glaciation in two areas. Morphologically distinct populations in the unglaciated areas of Alaska suggest that *S. malma* survived in that area. The present range of *S. malma* extends well south of the southern limits of glaciation and suggests that *S. malma* also survived south of the ice sheet on the west side of the continental divide. The present North American distribution of *S. malma* has probably been attained by both freshwater and marine dispersion mainly from south of the ice sheet. *Salvelinus malma* is often found in headwater streams which are highly susceptible to piracy from other watersheds. Possibly *S. malma* reached the east slope of the Rocky Mountains by this means. The anadromous habit accounts for the wide coastal distribution of *S. malma*.

In North America *S. alpinus* probably survived the last Pleistocene glaciation in the unglaciated areas of Alaska, and south of the ice sheet in eastern North America. The present North American distribution of *S. alpinus* has probably been attained largely through marine dispersion from these centres.

ACKNOWLEDGMENTS

Financial support for this study was provided by the Arctic Institute of North America, and the Institute of Fisheries of the University of British Columbia. The author particularly wishes to acknowledge the advice and guidance of Dr C. C. Lindsey, whose patience and humour made three summers of isolated field work a pleasure. The assistance of D. R. Miller during the summer of 1958 is gratefully acknowledged. Dr P. A. Larkin criticized the manuscript. Dr W. B. Scott, Royal Ontario Museum, generously made available his collections. Messrs R. Burgner, Fisheries Research Institute; D. E. McAllister, National Museum of Canada; T. Merrill, United States Fish and Wildlife Service; and A. Welander, College of Fisheries, University of Washington all supplied specimens. Miss M. Jurkela and Mr T. Ueno provided translations of Russian and Japanese literature. The co-operation and hospitality of numerous members of the Alaska Department of Fisheries, the Fisheries Research Institute of the University of Washington, and the United States Fish and Wildlife Service, is gratefully acknowledged. The assistance of the staff at the University of British Columbia Computing Centre is also acknowledged.

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A summary of the meristic data on which this study is based. The localities are arranged in a south-north order. The latitudes and longitudes are approximate.

Locality	N Lat.	W Long.	Number of specimens	Gill rakers Range	Mean	Vertebrae Range	Mean	Pyloric caeca Range	Mean	Pores along lateral line Range	Mean
<i>S. malma</i> —SOUTHERN FORM											
Gilfer Cr.	48° 30'	114° 05'	3	5-6+11-12	5+11	60-66	63.2	25-30	27.6	124-133	128.1
Logging Cr.	48° 30'	114° 10'	2	3-5+11-12	4+11	60-66	63.2	31-37	34	129-131	130
Fish Cr.	48° 30'	114° 10'	2	4-6+10-11	5+11	60-66	63.2	26-27	26.5	127-132	128.8
Sage Cr.	49° 10'	115° 07'	15	5-7+10-12	6+11	62-66	64	26-34	30	114-138	125.2
Sumallo R.	49° 17'	121° 14'	30	6-8+10-12	7+10	62-66	64.9	20-32	24.1	114-138	128.3
Pitt L.	49° 20'	122° 35'	6	4-8+11-12	6+11	...	...	19-24	22.1	126-131	128.9
Chehalis L.	49° 25'	122° 02'	17	4-8+10-12	6+11	...	...	22-32	24	120-135	127
Homathko R.	51° 00'	124° 55'	4	6+10-11	6+10	...	...	23-32	28.7	...	...
Cuthead L.	51° 10'	115° 45'	20	4-7+10-11	6+10	60-66	63.8	21-33	26.2	114-142	129.1
Adak I.	52° 00'	176° 40'	30	5-9+10-12	6+11	60-65	64.4	20-31	27.6	112-142	127
Ocean Falls	52° 40'	127° 35'	36	5-8+9-11	6+10	59-65	64.3	19-32	24.2	105-140	126.8
Cottonwood R.	53° 00'	122° 32'	15	4-6+10-12	5+11	58-66	63.4	23-32	28	123-137	130
Peace R.	56° 08'	121° 05'	5	5-7+10-12	6+11	62-65	63.9	23-32	27.1	121-140	132
Bowser L.	56° 30'	129° 30'	9	5-6+10-11	5+11	57-66	63.3	22-32	29	126-137	130
Fraser L.	57° 15'	154° 09'	38	4-8+8-12	5+10	62-66	64	26-47	35.4	117-140	127
Karluk L.	57° 23'	154° 05'	33	4-8+8-12	7+11	62-66	64	24-34	28.1	111-133	124
Midarm L.	58° 11'	152° 25'	30	6-8+11-12	7+11	58-66	64.1	25-36	27.8	115-138	123
Taku R.	58° 32'	133° 52'	25	5-8+10-12	7+10	60-66	64.2	21-31	27	115-141	130
Saltat Cr.	59° 36'	136° 29'	30	6-8+9-12	7+10	59-65	63	19-40	25.8	113-141	128.3
Kellsall L.	59° 48'	136° 32'	3	7-8+9-11	7+10	61-65	63	21-27	24.9	122-139	128
Swan L.	59° 53'	131° 24'	2	5-6+11	5.5+11	64	64	31-33	32	131-134	132.5
Little L.	60° 00'	130° 30'	4	5-7+10-12	6+11	64-66	65	23-26	25.2	103-125	118
Partridge Cr.	60° 00'	131° 50'	6	5-7+9-11	5+11	64-66	65.1	26-33	27.8	105-130	120
Kenai R.	60° 28'	151° 24'	1	...	8+12	...	65	...	27	...	128
Upper Trail L.	60° 31'	149° 24'	2	7-8+12	7.5+12	...	65	27-28	27.5	118-127	122.5
Summit L.	60° 37'	149° 31'	30	5-8+10-12	7+11	60-66	64.2	22-46	31	116-139	129
Turnagain Arm	60° 57'	149° 21'	20	5-8+9-12	7+10	57-66	64.1	16-27	20.2	110-135	124.2
Chena L.	61° 32'	144° 26'	5	8+10-12	8+11	59-65	64.1	21-26	24	129-143	135
<i>S. malma</i> —NORTHERN FORM											
Brooks L.	58° 22'	156° 00'	20	7-10+11-14	9+12.6	67-69	68	21-36	27.9	106-142	132.6
Hansen Cr.	59° 12'	158° 35'	30	8-10+11-14	9+12.9	66-70	67.6	21-30	26.7	111-140	128.7
Salmon L.	64° 50'	165° 00'	30	7-10+11-14	9+12.8	65-71	67.8	24-31	28	115-141	127
<i>S. malma</i> —DRY CREEK											
Dry Cr.	63° 41'	144° 00'	4	7-9+10-11	7+11	62-64	63	13-18	16	130-138	134

APPENDIX (continued)

<i>S. alpinus</i> —EASTERN ARCTIC									
Flaherty I.	55° 59'	79° 00'	10	9-13+14-17	11+16	...	...	30-52	44.7
Nain	56° 32'	61° 40'	3	9-11+15-16	10+15.7	...	...	40-44	42.6
Ft. Chimo	58° 15'	68° 05'	1	...	...	...	...	...	...
Merewether Crat.	61° 13'	73° 40'	10	9-12+15-17	11+16	64-67	66	31-47	36.9
Term Pt.	61° 51'	93° 00'	15	9-12+14-17	11+15.7	...	...	30-46	41
"Shona" L.	63° 30'	68° 50'	10	8-10+14-17	9+16	...	...	34-48	43.7
Armit L.	64° 06'	91° 32'	15	9-12+15-17	11+16	...	...	35-48	44
Sapuladjuk	64° 18'	76° 30'	10	9-12+14-17	10+16	...	...	35-47	42
Beverly L.	64° 35'	100° 38'	1	...	10+16	...	...	44	44
Beechey L.	65° 12'	106° 28'	2	10-13+16-17	11.5+16	...	...	40-46	43
MacDougal L.	65° 59'	98° 34'	2	11-12+17-18	11.5+17.5	...	...	45-47	46
Kathawachaga L.	66° 11'	111° 08'	16	9-12+16-19	11+18	65-68	67	38-58	45
Nettilling L.	66° 18'	70° 40'	8	9-12+15-16	11+15.7	...	...	29-46	39
Bloody Falls	67° 59'	115° 30'	10	9-12+13-16	11+15	...	...	26-51	46
Bernard Hb.	68° 48'	116° 10'	11	10-13+14-17	12+15.4	...	...	36-53	45
King William I.	69° 00'	98° 10'	1	...	10+16	...	...	...	46
Pond Inlet	70° 31'	77° 25'	1	...	12+17	...	66	...	...
Resolute Bay	74° 43'	94° 20'	6	9-11+14-17	10+16	...	...	36-47	41
Devon I.	76° 00'	86° 00'	2	9-11+15	10+15	...	...	42-47	44.5
Mould Bay	76° 12'	119° 09'	7	10-13+16-18	11+16.7	...	...	41-46	44
South Fiord	79° 24'	91° 55'	4	+15-18	+16	...	...	...	...
Victoria L.	81° 49'	70° 30'	1	...	12+16	...	Data courtesy K. E. Ricker	...	...
						67	67	...	38
								...	131
<i>S. alpinus</i> —BERING SEA AND WESTERN ARCTIC									
Nuivak I.	60° 00'	167° 00'	2	8-10+13-14	9+13.5	...	68	30-31	31.5
St. Matthews I.	61° 20'	172° 30'	10	8-11+12-14	9+13	...	...	28-44	30
Aniak R.	61° 35'	159° 40'	7	8-10+12-15	9+13	66-67	66.5	24-31	27
Tolstoi L.	63° 10'	157° 45'	30	7-10+12-15	9+13.7	...	...	23-32	27.8
St. Lawrence I.	63° 17'	169° 00'	40	7-11+12-14	9+13	...	...	21-35	28
Unalakleet R.	63° 52'	160° 55'	2	10+13-14	10+13.5	...	...	23-33	28
Nome R.	64° 28'	165° 20'	1	...	9+12	...	...	...	24
Nulato R.	64° 40'	158° 05'	3	9-10+13-14	9+13.3	...	...	20-27	23
Pt. Clarence	65° 10'	166° 30'	1	...	9+13	...	...	...	...
Pt. Hope	68° 20'	167° 00'	2	...	9+13	...	...	...	...
Aklavik	68° 20'	134° 30'	1	...	10+13	...	...	...	35
Chandler R.	69° 27'	151° 25'	1	...	10+14	...	...	...	...
Collison Pt.	69° 35'	139° 07'	2	11+12-13	11+12.5	...	...	28-31	29.5
Herschel I.	69° 35'	139° 00'	3	10+12-14	10+13	...	...	29-35	32.3
Oliktok Pt.	70° 30'	149° 50'	1	...	10+14	...	...	...	...
Elson Lagoon	71° 15'	156° 10'	3	...	9+13	...	...	28-30	29
<i>S. alpinus</i> —BRISTOL BAY AND GULF OF ALASKA									
Fraser L.	57° 15'	154° 10'	54	8-11+12-16	9+15	65-69	67	36-55	42.9
Karluk L.	57° 23'	154° 09'	32	8-11+12-16	9+14.6	65-69	67	35-57	44.3
Brooks L.	58° 22'	156° 00'	1	...	11+14	...	...	...	43
Aleknagik L.	59° 15'	158° 35'	30	8-10+12-17	9+15.1	66-71	67.6	29-74	52.5
Nerka L.	59° 25'	159° 00'	30	8-10+13-16	9+15.5	66-71	67.6	37-64	49
Idavain L.	59° 45'	156° 00'	4	8-10+14-16	9+14.7	...	...	...	...
Kisaralik L.	60° 28'	159° 20'	5	9-11+15-16	10+15.5	...	...	40-59	47

Detection of Incomplete Reporting of Tags^{1,2}

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ABSTRACT

A table is presented which gives the total number of tags that must be recovered in order to have a prescribed probability of discovering non-reporting by fishermen of a certain percentage of recaptured tags when a portion of the catch or of the effort is inspected by special observers. The table gives the required sample sizes for probabilities of detection of 0.50, 0.80, 0.90, 0.95, and 0.99 at various levels of catch inspection. The table may also be used to find the sample size needed to detect with prescribed probability a differential mortality between two identifiable groups of fish whose initial numbers are known. A number of examples of the use of the table are included.

INTRODUCTION

WHEN THE PRIMARY objective of a tagging or marking experiment is to estimate the rate of exploitation of a population supporting a fishery, it almost invariably follows that the actual recovery of the bulk of the tagged or marked fish is out of the hands of the investigators conducting the experiment. A major part of the responsibility of detecting and reporting recaptures of tagged fish must be entrusted to the commercial, sport or native fishermen who harvest the population.

Attempts to enlist the cooperation of the fishermen and to increase their effectiveness in recovering tags have ranged from educational programs to various reward schemes. Measures aimed at overcoming possible disinterest on the part of the fishermen and increasing their incentive to search for and to turn in tags have been particularly imaginative. For example, for returning a tag to the Inter-American Tropical Tuna Commission, the fisherman receives \$1 and a chance in an annual \$300 drawing (Schaefer, 1958). The Fisheries Research Institute at the University of Washington has approached the motivation problem in a forthright manner by proffering a reward of \$25 for the return of both fish and attached tag for recoveries of tagged salmon released in the North Pacific; this was accompanied by 2-fold increase in the percentage of tags returned (personal communication from Allan Hartt). To attribute this increase solely to the change in the value of the reward (from \$5 to \$25) is an oversimplification of a highly complex problem but the magnitude of the increase does lead to interesting speculation.

¹Received for publication March 6, 1961.

²This research was sponsored by the National Science Foundation under grant No. G-10365.

Recovery programs that depend on voluntary tag reporting by sports fishermen appear to be subject to particularly high levels of non-response error. Angler response also appears to be highly sensitive to a variety of factors and is apt to fluctuate markedly depending on the accompanying circumstances, e.g., in one of two studies conducted in Massachusetts, Mullan (1959) found a 60% non-response for mandible tags on trout; and in the other, Stroud and Bitze (1955) estimated a 25% non-response for strap and cheek tags on warm-water species. A recent article by McCammon and LaFaunce (1961) should be consulted for a more complete discussion of the incomplete reporting problem for freshwater sport fisheries.

While rewards and other such measures decrease the possibility of non-reporting of tags, each tagging experiment should be so designed as to contain some provisions for testing the assumption that all of the recaptured tags are turned in. The most direct method of testing this assumption is to have trained observers examine a portion of the catch. A sampling program of this sort may be objectionable because of the manpower requirements and because of the cost involved but it would seem to be unavoidable except in special circumstances.

The purpose of this note is to provide the biologist planning a tagging experiment with a preliminary guide to help him decide how many tags should be put out and how much of the catch should be inspected to be reasonably sure of discovering non-reporting of a certain magnitude. When the total outlay for the tagging experiment is fixed the table furnished here should also be an aid in allocating personnel and resources to best advantage between the tagging and recovery phases of the experiment. There may be a temptation to sample the catch for marks in a perfunctory manner and to conclude that incomplete reporting is not a serious problem unless a sizeable difference between the tagged to untagged ratios for the inspected and uninspected portions of the catch shows up. Table I shows that if only "token" catch sampling is carried on, there is a rather large chance that a significant amount of incomplete reporting will not be detected. Or, to view the problem in a slightly different perspective, if we wish to maintain the same assurance of detecting incomplete reporting, a substantial increase in the numbers of fish tagged may be required to offset a decrease in the proportion of the catch inspected.

THEORY AND METHODS

If incomplete reporting is extensive, the apparent rate of exploitation or the apparent size of the population as calculated from the tag returns may be seriously biased. The true rate of exploitation is equal to the apparent rate divided by the fraction of tags that are reported (Ricker, 1958). A convenient term for this fraction is the *reported ratio* which has been defined as (to paraphrase Atwood and Geis, 1960): the fraction of the total number of tagged or marked fish caught that are subsequently reported to the research agency.

In the development that follows it is assumed that the reported ratio remains constant throughout the experiment and over the entire area in which the

recoveries are made. If these conditions are not met, it may be possible to subdivide the recoveries into groups so that the reported ratio for each sub-division is constant.

The need for such stratification should obviously be explored if the recoveries are made by nationals of several countries in an internationally fished area (Beverton and Holt, 1957, p. 200), or the publicity given to the experiment is unevenly distributed over the exploited area. A time stratification might be called for if there is reason to suspect a tag may be retained by the fishermen as a talisman when it is first introduced (Idyll, 1952; Rounsefell and Everhart, 1953). A number of specific examples of areal and temporal variations in the reported ratios for banded waterfowl are presented by Atwood and Geis (1960).

A natural formulation of the problem of detecting incomplete reporting is as a test of the hypothesis that the reported ratio is equal to 1, against the alternative that the reported ratio is less than 1. The probability of detecting a reported ratio that is less than 1 with such a test (this probability is generally referred to as the "power" of the test) will be examined using the following notation:

ρ reported ratio (tags reported $\div$ tags captured)

f_i number of standardized units of gear in the i th class ($i = 1, 2$)

C_i catch in numbers in the i th class

r_i number of tags recovered in the i th class ($r = r_1 + r_2$)

s_i number of tags reported from the i th class ($s = s_1 + s_2$)

t number of tags liberated

N number of fish in population at time of tagging

Z standardized normal variate, $\Pr(Z \geq z_{1-\alpha}) = \alpha$

α level of significance of the test, or the probability of rejecting the null hypothesis when true, i.e., concluding that $\rho < 1$ when in fact $\rho = 1$

β probability of concluding that ρ is equal to 1 when in fact ρ is less than 1

More adequate definitions of the statistical terms may be found in any standard text on statistics, e.g., see Chapter 7 of Dixon and Massey (1957).

Observe that α and β are the respective probabilities of two opposite types of error:

α is the probability of erroneously concluding that some tags are not reported when in fact all are reported.

β is the probability of failing to detect that some tags are not reported when in fact only the fraction ρ of them is reported.

It is necessary to specify acceptable levels for both of these in order to compute the number of fish that should be marked.

The procedure outlined below presupposes the feasibility of classifying either the catch or fishing effort into two categories, one of which has a known reported ratio of unity or nearly so, while the other has an unknown reported ratio that is to be estimated from the tag recoveries. In practice, the former category would

be defined as the fraction of the catch or the effort inspected by special observers; or, possibly, as the units of gear operated by fishermen who, by virtue of special training, long experience, or a keen interest in the experiment, could be relied upon to turn in all of the tags that appear in their catches. The sampling for tags might easily be coordinated with the collection of other biological data. For example, the International Pacific Halibut Commission at present assigns a biologist to each of a number of the vessels in the halibut fleet. One of the biologist's routine duties is to inspect the catch as it is brought aboard (personal communication from R. J. Myhre).

CATCH SAMPLING

A simple probability model may be formulated in terms of catch inspection. For most commercial fisheries large catches (C_i 's) and low tag ratios (t/N 's) would be expected. If it is assumed that the same tag ratio applies to both inspected and uninspected classes and that the tag ratio within each class remains constant for the duration of the experiment, the number recovered in each class should be approximately distributed according to a Poisson law (e.g., see Chapman, 1954), i.e.:

$$\Pr(r_i) = \left(\frac{C_i t}{N}\right)^{r_i} \frac{e^{-C_i t/N}}{r_i!} \quad i = 1, 2 \quad (1)$$

Now by assumption, $s_1 = r_1$, and it is reasonable to assume further that given r_2 , s_2 is binomial (r_2, ρ), i.e.:

$$\Pr(s_2|r_2) = \binom{r_2}{s_2} \rho^{s_2} (1-\rho)^{r_2-s_2} \quad (2)$$

By a well known result (e.g., see Feller, 1957, p. 269), s_2 is Poisson $\left(C_2 \frac{t}{N} \rho\right)$. It then follows that:

$$\Pr(s_1|s) = \binom{s}{s_1} \left(\frac{C_1}{C_1 + \rho C_2}\right)^{s_1} \left(\frac{\rho C_2}{C_1 + \rho C_2}\right)^{s_2} \quad (3)$$

If the assumption that the tag ratio remains constant during the entire season is permissible, the catch inspection scheme is highly flexible, e.g., all of the fish landed during the first part of the season may be inspected and none of those during the latter part of the season or vice versa. It will be shown below that this assumption may be weakened somewhat provided that catch sampling is carried on in a specified manner. If we assume that the season can be divided into J intervals so that the tag ratio ($= t_j/N_j$ for $j = 1, 2, \dots, J$) remains constant within each interval, then:

$$\Pr(r_{ij}|t_{ij}, N_j) = \frac{e^{-C_{ij} t_j/N_j} \left(\frac{C_{ij} t_j}{N_j}\right)^{r_{ij}}}{r_{ij}!} \quad (4)$$

for $i = 1, 2$ and $j = 1, 2, \dots, J$

Under these conditions it is necessary to sample the same fraction of the catch in each of the J intervals. Denoting the constant fraction of the catch inspected by λ it can be easily shown (as above) that:

$$\Pr(s_{1..}|s_{..}) = \binom{s_{..}}{s_{1..}} \left(\frac{\lambda}{\lambda + \rho(1-\lambda)} \right)^{s_1} \left(\frac{\rho(1-\lambda)}{\lambda + \rho(1-\lambda)} \right)^{s_2} \quad (5)$$

where the dot notation is used to indicate summation over a subscript, i.e.:

$$s_{1..} = \sum_{j=1}^J s_{1j}$$

Although the Poisson distribution probably applies to most fisheries situations cases may arise, e.g., (when t/N is not small), in which the probability of r_i recoveries may be more adequately approximated by a binomial law, i.e.:

$$\Pr(r_i) = \binom{C_i}{r_i} \left(\frac{t}{N} \right)^{r_i} \left(1 - t/N \right)^{C_i - r_i} \quad (6)$$

Equation (6) is equivalent to assuming that two independent random samples of sizes C_1 and C_2 respectively, are drawn from an infinite population for which probability of recovering a tag is t/N . Assuming as before that $s_1 = r_1$ and s_2 , given r_2 , is binomial (r_2, ρ), we have:

$$\Pr(s_i) = \binom{C_i}{s_i} \left(\frac{\rho_i t}{N} \right)^{s_i} \left(1 - \frac{\rho_i t}{N} \right)^{C_i - s_i} \quad i = 1, 2 \quad (7)$$

where $\rho_1 = 1$ and $\rho_2 = \rho$. When the samples taken at all stages are chosen randomly, the exact probability distribution of the recoveries reported by the fishermen could be constructed from the observation that the probability of a total of r recoveries, when a sample of size C is taken, is hypergeometric (Chapman, 1951); given r , C and C_2 , the conditional probability of r_2 is again hypergeometric, and the conditional distribution of s_2 given r_2 is binomial (r_2, ρ). Unfortunately, this construction leads to equations that are difficult to manage algebraically.

If the observations are arranged in the usual 2 by 2 table, the chi-square statistic can be used to test the hypothesis $H: \rho = 1$. Since the alternative ($\bar{H}: \rho = \rho_a < 1$) is one-sided, we would modify the usual test slightly by only rejecting H when $s_1/C_1 > s_2/C_2$ and the chi-square statistic exceeds $\chi^2_{1-2\alpha}$ instead of the usual $\chi^2_{1-\alpha}$. The limiting power of the chi-square test has been studied by Mitra (1958) and he gives the formulae needed for the power computations and examples of their use. For small numbers of recoveries and small catch sizes the hypothesis that a tag is equally likely to be returned from the un-inspected as from the inspected portions of the catch could be tested by Fisher's exact test (Fisher, 1954). Tables and charts of the exact power of this test have been prepared by Bennet and Hsu (1960). Hsu (1960) gives a normal approximation that can be used for power computations when large sample sizes are involved. Another avenue of attack when larger samples are available would be to use the fact that $y_1 = 2 \arcsin \sqrt{s_1/C_1}$ measured in radians has an approximate normal ($2 \arcsin \sqrt{\rho_1 t/N}, 1/C_1$) distribution. A detailed exposition of the power computa-

tions for the angular transformation and an arcsin table are available in Brownlee (1960).

The present discussion will be restricted to the case where the conditional distribution of the recoveries in a given class can be represented by equation (3). It may be asked what would happen if the Poisson distribution was erroneously assumed when in fact the binomial distribution given in equation (6) did apply. The required sample size as computed from Table I would then be conservative and the true power of the test would exceed the nominal power. A heuristic proof of this statement would be that under the null hypothesis the binomial probability given in equation (3) is replaced by the hypergeometric, i.e.:

$$\Pr(s_1|s) = \frac{\binom{C_1}{s_1} \binom{C_2}{s_2}}{\binom{C}{s}}$$

which has a smaller variance. Since the use of this technique in practice will involve a number of approximations, it is doubtful whether it would be worth the trouble to go through the more exact and more laborious power calculations.

EFFORT SAMPLING

For many fisheries the units of gear are the natural sampling units and effort sampling may actually involve less effort on the part of the research agency. There also may be some advantage in trading the assumptions concerning relations between the tagged and untagged portions of the population which are needed for the catch inspection method for parallel assumptions about the relationship between the tagged population and the fishing effort. Assume that the f_1 units of gear, which have a reported ratio of one, differ in no other way from the other units of gear. Assume further that the fishery is continuous with respect to the tagged populations (see Beverton and Holt, 1957) and that

$$\Pr \left(\begin{array}{c} \text{tag is recovered by the} \\ \text{research agency between} \\ \text{times } t \text{ and } t + dt \end{array} \right) = q(f_1 + \rho f_2) e^{-[q(f_1 + f_2) + X]t} dt \quad (8)$$

where X is an instantaneous rate which represents all factors other than the fishery which act to reduce the tagged population and q = ratio of the instantaneous rate of fishing mortality to the fishing intensity. For ρ , f_1 , f_2 , and X constant, by time $t = T$, a given tag will either have been recovered from the f_1 units of gear, the f_2 units of gear or will not have been recovered. The probabilities of the three possibilities are equal to:

$$\begin{aligned} & \frac{qf_1}{F + X} \left(1 - e^{-(F + X)T} \right) \\ & \frac{q\rho f_2}{F + X} \left(1 - e^{-(F + X)T} \right) \\ & 1 - \frac{q(f_1 + \rho f_2)}{F + X} \left(1 - e^{-(F + X)T} \right) \end{aligned}$$

respectively, where $F = q(f_1 + f_2)$. Given that a tag has been reported, the probability that it was taken by fishermen in the first class is then binomial, i.e.:

$$\Pr(s_1|s) = \binom{s}{s_1} \left(\frac{f_1}{f_1 + \rho f_2} \right)^{s_1} \left(\frac{\rho f_2}{f_1 + \rho f_2} \right)^{s-s_1} \quad (9)$$

which is completely analogous to the corresponding results for catch sampling, cf., equation (3).

The parameter q measures "catchability" which in actuality may vary considerably during a long season or over several seasons. If the time scale is divided into J intervals and $q(t) = q_j$ for $t_{j-1} \leq t \leq t_j$, $j = 1, 2, \dots, J$, it can be easily shown (following Chapman, 1960) that for a given tag the expected probability of recovery by the research agency by time $t = T_J$ is:

$\Pr(\text{recovery by fisheries agency}) =$

$$\sum_{j=1}^J \frac{q_j(f_1 + \rho f_2)}{X + q_j F} e^{-(X T_{j-1} + F \sum_{i=0}^{j-1} q_i \Delta_i)} \left(1 - e^{-[X + q_j F] \Delta_j} \right) \quad (10)$$

where $\Delta_j = t_j - t_{j-1}$. By simply deleting ρf_2 in equation (10) we obtain an expression for the probability that the recapture was made by the fishermen in the first class. Thus the conditional probability of s_1 given s is again given by equation (9) showing that so long as the same fraction of the effort is inspected during each of the J intervals, variations in catchability can be ignored. Of course, the same statement also applies to variations in the number of units of gear since the fluctuations in the levels of fishing intensity could be incorporated in the parameter q .

COMPUTATION OF SAMPLE SIZE

The null hypothesis, $H_0: \rho = 1$, would be doubted if the proportion of tags recovered from the inspected class is too high in relation to the proportion of the catch or the amount of gear in this class. Using the normal approximation of the binomial distribution, the well known most powerful one-sided test would be to reject H_0 if $s_1 \geq s_R$ where:

$$s_R = z_{1-\alpha} \sqrt{s p_0 q_0} + 1/2 + s p_0 \quad (11)$$

$$p_0 = \frac{f_1}{f_1 + f_2} \text{ or } = \frac{C_1}{C_1 + C_2}$$

$$q_0 = 1 - p_0$$

if this expression happens to be an integer. If it is not, s_R is taken to be the nearest integer which is larger. The power of the test against a specific alternative would be the probability of rejecting H_0 when $\rho = \rho_a < 1$. Again, approximating the binomial distribution by the normal, the number of recoveries needed to test H_0 at pre-set values of α and β for different ρ 's can be expressed as:

$$s = \frac{(z_{1-\beta} \sqrt{p_1 q_1} + z_{1-\alpha} \sqrt{p_0 q_0})^2}{(p_1 - p_0)^2} \quad (12)$$

$$p_1 = \frac{f_1}{f_1 + \rho f_2} \text{ or } = \frac{C_1}{C_1 + \rho C_2}$$

$$q_1 = 1 - p_1.$$

Values of s as a function of the reported ratio and the fraction of the total catch inspected, $C_1/(C_1 + C_2)$, or of the total effort, $f_1/(f_1 + f_2)$, for which the reporting is known to be complete, are given in Table I. The tabled values have low accuracy for small values of s where the normal approximation to the binomial distribution is not too close. These errors are of little importance for larger s 's.

EXAMPLES

The following four examples will illustrate the use of Table I.

EXAMPLE 1

A biologist wants to be 99% sure of detecting non-reporting of 20% or more of the tags recovered by a commercial fishery. From past experience he knows that at least 30% of the tags released will be recovered. Twenty-five percent of the fishermen agree to attend a special course of instructions and cooperate fully in this experiment. If α (the probability of mistakenly concluding that the reported ratio, ρ , is less than 1) be set at 0.10, how many tags should be liberated?

SOLUTION: In Table I, for $\rho = 0.80$, $f_1/(f_1 + f_2) = 0.25$, $\alpha = 0.10$ and $1 - \beta = 0.99$, s is found to be 1340. To solve for t , the number of tags that must be put out when the 30% recovery estimate refers to recaptured but not necessarily reported tags, note that r , the number of tags we would expect to be recaptured, can be written $r = ut$, where u is the rate of exploitation (see Ricker, 1958, p. 20). Then s , the number of tags turned in, should be:

$$s = u \left(\frac{f_1}{f_1 + f_2} + \frac{\rho f_2}{f_1 + f_2} \right) t$$

Substituting the values given above:

$$1340 = 0.30 \left(\frac{1}{4} + (0.80) \frac{3}{4} \right) t$$

$$t = \frac{4(1340)}{(0.30)(3.40)} = 5255$$

However, the 30% recovery estimate could have been based on the percentage of tags reported in the past. In this case, $\rho u = 0.30$ or $u = 0.30/0.80$. We now expect the number of tags reported to be:

$$s = \frac{0.30}{0.80} \left(\frac{1}{4} + (0.80) \frac{3}{4} \right) t$$

Solving for t :

$$t = \frac{4(0.80)(1340)}{(0.30)(3.40)} = 4204$$

The point of this example is that the tagging program should be designed to return at least 1340 tags to the research agency.

The second example illustrates a situation where there may be a differential between the costs of catch sampling and effort sampling.

EXAMPLE 2

A biologist wants to estimate the percentage of marks detected and reported by sportsmen and would like to be 90% sure of discovering a reported ratio of 80% or lower. Two thousand marked trout have been released in a large lake shortly before the opening of the fishing season and an unknown portion of them would be expected to survive until opening day. Assume:

- (i) the unmarked and marked members of the population are equally vulnerable to capture;
- (ii) a reliable estimate of the total effort and the total catch for each week of the season is available;
- (iii) the "catchability" of the trout is constant within a week but may vary from week to week;
- (iv) no immigration or reproduction occurs during the season and thus the size of the population in the lake declines steadily as the catch mounts.

The biologist must decide whether to sample the catch or the effort to estimate the reported ratio. We will consider sampling to be largely a problem of providing coverage for the areas of access to the lake and that the cost would be roughly proportional to the percentage of the total effort interviewed on a given day regardless of the numbers of fishermen involved. In such a situation it may be relatively inexpensive to sample 10% or 20% of the fishermen using the lake on a given day, but the costs would be expected to increase rapidly as the percentage of fishermen included in the sampling was increased.

The total number of fish recovered from sampling a fixed percentage of the fishermen would, of course, tend to drop in the latter part of the season because of the drop in the numbers of fish in the lake and the concomitant decrease in the numbers of fishermen. For example, the total catch during a 5-week season may be 100,000 but the majority of these fish, say 63,000, may be taken during the first week of the season. Sampling one-half of the effort expended during the first week (which represents a smaller portion, say 20%, of the total season's effort; e.g., if a total of 25,000 units of effort were expended during the entire season, 10,000 or 40% of these fished during the first week) would then provide 31.5% of the total catch. On the other hand, inspection of a straight 20% of the effort expended each week would be expected to yield only 20% of the catch. As the marked ratio remains constant the catch can be inspected anytime during the season. Clearly the optimum time to inspect the catch is during the first part of the season when both the intensity and catch per unit of effort are highest; we will assume the entire catch sample will be taken during the first week.

However, effort sampling is not so flexible. Because catchability and population size vary, a constant percentage of each week's effort must be sampled. Effort sampling does not require assumption (i) since only the relationship between the effort and the marked population is involved. However, (i) is replaced by the assumption that the percentage recovery is directly proportional to the fishing intensity in any interval.

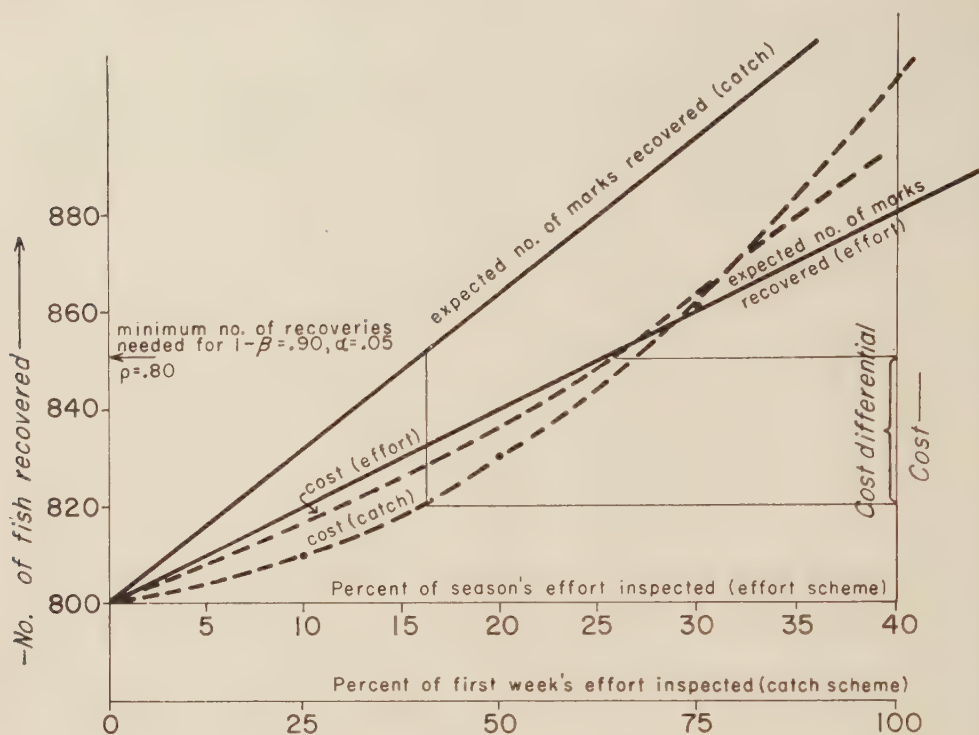


FIG. 1. Comparison of the costs of catch and effort sampling for a sports fishery.

The relevant factors that must be considered when evaluating the two sampling schemes are illustrated in Fig. 1. An arbitrary number (taken to be 1000 here) must be assigned to the expected total number of marked fish recovered to plot the two "expected number-of-recoveries" lines. The required number of recoveries was taken from Table 1, using $\alpha = 0.05$, $\beta = 0.10$, $\rho = 0.80$ for the optimum $f_1/(f_1 + f_2)$ and $C_1/(C_1 + C_2)$ ratios. For the cost curves shown, catch sampling is most economical. A different choice of cost curves might reverse the verdict.

The next two examples will illustrate the use of Table I in other areas of fisheries research.

EXAMPLE 3

Suppose the experiment described in Example 2 was carried out and reported ratio of unity was found. The following year the hatchery conducts an experiment to determine the advisability of early pre-season stocking as opposed to plants made just before the onset of fishing. Assume that if the trout can be released two months before the opening of the season, the capacity of the hatchery (and the number of fish stocked) can be increased by 10%. Thus if the survival rate of the early pre-season releases is greater than 0.909 an

increase in the catch should result from early planting (ignoring possible differences between the growth rates of early and late plants).

To estimate this survival rate ($= q$), N_E fish are released in the early plant and N_C fish in the late plant. Assume that the survival of the late plant is one³ and that the hypothesis of interest is, $H: q = 1$, *vs.* the alternative $\bar{H}: q = q_1 < 1$. The probability of rejecting H should be high when $q_1 \leq 0.90$. Taking $\beta = 0.01$ and $\alpha = 0.05$, how many recoveries are needed and what is the approximate optimum ratio of $N_C/(N_C + N_E)$? The exact optimum ratio will usually lie between two of the ratios given in Table I. However, since in the neighborhood of the optimum ratio, the required sample sizes change slowly, the tabulated values will suffice for most practical purposes.

SOLUTION: In Table I for $\rho (= q) = 0.90$, $\alpha = 0.05$ and $\beta = 0.01$ the minimum number of recoveries is found to be 5684 when $N_C/(N_E + N_C) = 0.5$. If the expected recovery is at least 60%:

$$N_C + q_1 N_E = \frac{5684}{0.6}$$

Or, setting $N_E = N_C$:

$$N_C = \frac{5684}{(0.6)(1 + q_1)} = 4986$$

EXAMPLE 4

An experiment to determine if the survival rate of downstream migrant salmon is significantly reduced by passage over a dam might involve the release of one group (experimental) of fingerlings in the forebay and another group (control) in the tail-race of the dam. Fyke nets or other such gear would be employed some distance downstream to recover the fingerlings. Setting N_C and N_E equal to the respective numbers of controls and experimentals released, n equal to the total number of recoveries and q equal to the survival rate of the experimentals, test the $H: q = 1$ *vs.* $\bar{H}: q = q_1 < 1$. If the experimenter wishes to be 80% sure of detecting a mortality of 5% or greater and uses an $\alpha = 0.05$, how many recoveries are required?

SOLUTION: Entering Table I with $\rho (= q_1) = 0.95$, $\alpha = 0.05$, $\beta = 0.20$; n is found to be 9402 for $N_C/(N_E + N_C) = 0.5$. In this case the experimenter has the option of varying either the number of fingerlings released or the recovery effort to obtain the desired number of recoveries. The number of fish recovered may be proportional to the fraction of the total cross-sectional area of the stream covered by nets at the recovery site and, if so, the cost of recovering a given percentage of the fish released at the dam could then be easily computed. The relative costs of sampling and of obtaining and marking fingerlings would then determine the optimum allocation of funds to minimize the total cost of the experiment.

³A survival rate of 1 was assumed for simplicity. The method illustrated is equally applicable if the survival of the late plant was taken as γ where $0 < \gamma < 1$ and the null hypothesis and the alternative were $H: q = \gamma$ and $H: q = q_1 < \gamma$, respectively.

COMMENTS

The plan presented here for estimating incomplete reporting should not be confused with the plan of examining the catch for tags that the fishermen failed to remove. Such "posterior" examinations are quite valuable in helping to bridge the gap between the number of tags the fishermen catch and the number that are eventually returned to the research agency but do not measure nonresponse error.

Examination of the uninspected portion of the catch for tags not removed by the fishermen (supposedly the inspected portion of the catch will contain no tags) is a means of separating the incomplete reporting bias into its components. One component is the fisherman's failure to remove the tag from the catch and the other is the fisherman's failure to return recovered tags to the research agency.

The required sample sizes tabulated in Table I demonstrate the difficulty in detecting incomplete tag reporting even when a number of demanding assumptions are satisfied. The evaluation and interpretation of tagging results usually requires many more assumptions, e.g., that the immediate mortalities suffered as a direct result of the tagging operation are negligible, that the fish's normal behavior pattern has not been drastically altered by the application and presence of the tag, that the recovery gear is not selective for tagged fish, etc. In many cases the experimental results will not provide an adequate test of these assumptions. Careful advance planning and execution of tagging experiments are required if the results are to be meaningful. The design of the experiment must take into account the nature of the fish and of the fishery and the experiment should involve substantial numbers of fish and an extensive recovery operation.

ACKNOWLEDGMENTS

The author would like to gratefully acknowledge the stimulating guidance and encouragement provided by Dr Douglas G. Chapman of the Department of Mathematics of the University of Washington during the preparation of the paper. Mr Charles Junge of the Fisheries Research Institute suggested the application given in Example 4 and contributed a number of other helpful ideas.

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TABLE I. Number of recoveries needed for prescribed probabilities of detecting incomplete reporting with various levels of catch inspection. Symbols are defined on page 819.

$$\alpha = 0.10$$

ρ	$1-\beta$	$C_1/(C_1 + C_2)$ or $f_1/(f_1 + f_2)$									
		.05	.10	.15	.20	.25	.30	.40	.50	.70	.90
.25	.50	6	4	4	3	3	4	4	5	9	28
	.80	24	14	11	10	10	9	10	11	17	51
	.90	39	23	18	15	14	14	14	15	23	66
	.95	54	31	24	20	19	18	18	19	28	80
	.99	88	50	37	32	29	27	26	28	40	109
.50	.50	39	23	18	15	14	14	14	15	23	66
	.80	136	76	56	47	42	39	38	39	55	147
	.90	210	116	85	71	63	58	55	56	76	201
	.95	284	156	114	94	83	76	71	73	97	252
	.99	453	246	178	146	128	117	108	109	143	365
.60	.50	84	47	36	30	27	26	25	27	38	106
	.80	276	151	110	91	80	74	69	71	95	247
	.90	421	229	166	136	120	110	101	102	134	344
	.95	564	305	221	180	158	144	132	133	172	436
	.99	888	478	344	280	243	221	201	200	256	639
.70	.50	197	109	80	66	59	55	52	53	72	191
	.80	615	332	240	196	171	156	143	143	186	469
	.90	925	498	359	291	253	230	209	208	266	662
	.95	1230	660	474	384	333	302	273	271	342	847
	.99	1917	1026	734	593	513	464	416	410	513	1256
.75	.50	322	176	128	106	93	86	80	81	108	278
	.80	981	527	380	308	268	244	221	220	280	696
	.90	1468	787	564	456	395	358	323	319	402	990
	.95	1943	1040	744	601	519	470	422	415	519	1272
	.99	3016	1609	1148	925	797	720	643	630	781	1895
.80	.50	568	307	222	182	159	145	133	134	173	439
	.80	1688	904	647	523	453	410	369	364	457	1121
	.90	2512	1341	958	772	667	602	539	529	658	1603
	.95	3314	1767	1260	1015	875	789	704	689	853	2065
	.99	5120	2725	1939	1558	1340	1207	1073	1046	1285	3093
.85	.50	1130	607	436	354	307	279	252	250	317	787
	.80	3290	1754	1251	1007	868	783	699	684	847	2052
	.90	4866	2590	1844	1482	1275	1148	1021	997	1225	2950
	.95	6401	3403	2420	1943	1670	1502	1333	1298	1590	3814
	.99	9845	5227	3712	2975	2554	2294	2031	1972	2402	5733
.90	.50	2832	1512	1079	869	750	677	605	593	736	1789
	.80	8074	4289	3048	2444	2100	1887	1672	1626	1985	4748
	.90	11881	6305	4475	3585	3076	2761	2442	2369	2880	6859
	.95	15579	8261	5859	4691	4022	3608	3186	3086	3743	8894
	.99	23864	12643	8959	7166	6138	5501	4850	4691	5669	13423
.95	.50	12548	6658	4724	3785	3246	2914	2576	2499	3036	7227
	.80	35080	18573	13151	10513	8999	8060	7097	6855	8262	19515
	.90	51367	27181	19237	15369	13149	11770	10352	9989	12013	28320
	.95	67153	35522	25132	20072	17167	15362	13503	13020	15641	36822
	.99	102459	54175	38312	30586	26148	23389	20540	19791	23732	55778

TABLE I (continued)

 $\alpha = 0.05$

ρ	$1-\beta$	$C_1/(C_1 + C_2)$ or $f_1/(f_1 + f_2)$									
		.05	.10	.15	.20	.25	.30	.40	.50	.70	.90
.25	.50	9	6	5	5	5	6	7	8	14	46
	.80	30	19	15	13	13	13	14	15	25	75
	.90	47	28	22	19	18	18	18	20	32	93
	.95	63	37	29	25	23	22	23	25	38	109
	.99	101	57	44	37	34	33	32	35	51	143
.50	.50	63	37	29	25	23	22	23	25	38	109
	.80	180	100	75	63	57	53	51	54	76	207
	.90	264	146	108	90	80	75	71	74	102	271
	.95	346	191	140	116	103	95	90	92	125	331
	.99	530	289	211	174	153	141	131	133	177	458
.60	.50	137	77	58	49	45	42	41	44	63	174
	.80	368	202	148	123	109	101	95	97	132	346
	.90	533	291	212	175	154	142	131	134	178	460
	.95	693	376	273	224	197	180	166	168	221	566
	.99	1048	566	409	334	291	266	243	244	315	794
.70	.50	324	178	131	109	97	90	85	87	119	315
	.80	827	448	325	266	233	213	196	197	257	653
	.90	1183	638	461	375	327	298	272	272	350	879
	.95	1524	820	590	479	417	379	344	343	437	1091
	.99	2281	1223	877	710	615	558	503	498	628	1549
.75	.50	530	289	211	174	153	141	131	133	177	458
	.80	1325	714	515	419	364	332	302	301	386	968
	.90	1883	1011	726	589	511	464	420	416	528	1310
	.95	2417	1296	929	751	651	590	532	525	662	1631
	.99	3600	1924	1375	1110	959	867	777	764	953	2328
.80	.50	935	506	366	299	261	239	219	220	285	722
	.80	2289	1227	880	712	617	560	505	499	630	1554
	.90	3234	1730	1237	999	864	781	701	690	863	2114
	.95	4137	2209	1578	1272	1098	992	888	872	1084	2641
	.99	6132	3268	2329	1874	1614	1455	1297	1269	1567	3788
.85	.50	1862	1000	718	582	506	459	415	412	523	1297
	.80	4473	2388	1705	1374	1185	1070	957	939	1166	2836
	.90	6287	3350	2387	1920	1654	1491	1329	1299	1604	3877
	.95	8016	4267	3037	2441	2100	1891	1682	1641	2018	4859
	.99	11827	6286	4468	3585	3080	2769	2456	2390	2922	7000
.90	.50	4666	2490	1777	1432	1235	1115	997	977	1213	2947
	.80	11012	5854	4162	3340	2871	2582	2291	2230	2730	6544
	.90	15398	8176	5807	4655	3997	3590	3179	3088	3764	8989
	.95	19572	10386	7371	5905	5066	4548	4022	3902	4743	11299
	.99	28752	15243	10808	8651	7415	6649	5870	5684	6886	16345
.95	.50	20671	10967	7782	6234	5348	4799	4243	4116	5000	11905
	.80	47983	25412	18000	14393	12324	11041	9727	9402	11345	26830
	.90	66770	35343	25021	19997	17114	15324	13487	13022	15682	27011
	.95	84619	44776	31689	25317	21660	19389	17053	16456	19791	46652
	.99	123797	65478	46319	36989	31632	28303	24871	23978	28788	67742

TABLE I (continued)

 $\alpha = 0.01$

ρ	$1-\beta$	$C_1/(C_1 + C_2)$ or $f_1/(f_1 + f_2)$									
		.05	.10	.15	.20	.25	.30	.40	.50	.70	.90
.25	.50	17	12	10	10	10	11	13	16	28	92
	.80	45	28	23	21	20	20	22	25	42	131
	.90	65	39	31	28	27	26	28	32	51	155
	.95	84	50	39	35	33	32	33	37	59	175
	.99	126	73	57	49	46	44	45	49	75	218
.50	.50	126	73	57	49	46	44	45	49	75	218
	.80	278	157	118	100	90	85	83	88	127	350
	.90	382	213	158	133	119	112	108	113	159	432
	.95	479	266	197	164	147	137	130	136	188	506
	.99	692	381	280	232	205	190	179	184	250	661
.60	.50	274	154	116	98	89	84	82	87	125	347
	.80	578	319	235	195	174	162	153	158	217	579
	.90	781	428	314	259	230	212	199	204	276	723
	.95	971	531	387	319	281	259	242	246	329	855
	.99	1385	753	546	448	393	360	332	336	441	1131
.70	.50	648	357	262	218	193	179	169	174	238	629
	.80	1312	713	518	425	373	342	316	320	422	1083
	.90	1751	948	686	561	490	449	412	414	539	1368
	.95	2162	1167	843	687	599	547	500	500	645	1629
	.99	3048	1640	1180	959	834	758	688	685	874	2181
.75	.50	1060	578	422	347	305	281	261	266	353	914
	.80	2110	1140	823	671	586	535	489	490	633	1597
	.90	2802	1509	1087	883	769	700	636	634	811	2029
	.95	3446	1852	1331	1080	938	852	772	767	975	2424
	.99	4835	2591	1857	1503	1302	1180	1063	1050	1323	3261
.80	.50	1869	1011	732	597	522	477	437	439	570	1444
	.80	3661	1966	1413	1145	994	903	817	811	1029	2555
	.90	4834	2591	1857	1502	1301	1179	1063	1050	1323	3261
	.95	5927	3172	2270	1834	1586	1435	1290	1271	1593	3909
	.99	8775	4419	3156	2544	2196	1984	1775	1743	2169	5282
.85	.50	3724	2000	1437	1165	1011	918	830	824	1045	2593
	.80	7184	3840	2744	2214	1913	1729	1550	1524	1902	4647
	.90	9441	5038	3595	2896	2498	2255	2015	1976	2452	5957
	.95	11537	6150	4383	3528	3040	2741	2445	2393	2958	7161
	.99	16035	8534	6074	4882	4201	3782	3364	3283	4036	9719
.90	.50	9332	4980	3554	2863	2470	2229	1993	1954	2424	5894
	.80	17752	9444	6720	5398	4643	4178	3714	3621	4445	10689
	.90	23221	12342	8773	7040	6049	5438	4824	4695	5742	13759
	.95	28291	15027	10674	8560	7351	6604	5851	5687	6938	16586
	.99	39150	20774	14743	11812	10134	9096	8044	7804	9488	22601
.95	.50	41348	21937	15566	12469	10696	9600	8487	8232	10002	23813
	.80	77628	41128	29142	23312	19969	17897	15779	15263	18444	43682
	.90	101102	53539	37919	30318	25958	23254	20483	19795	23878	56448
	.95	122823	65021	46037	36797	31496	28206	24830	23981	28893	68223
	.99	169262	89565	63386	50642	43326	38784	34111	32916	39588	93317

The Light Pickle Salting of Cod¹

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ABSTRACT

Salting theory for the light pickle salting of cod on a commercial scale is discussed and data are presented on the salt uptake with respect to time, temperature, and location in the tank. Variation of salt uptake by fish was examined and the proportion of top-quality fish, in terms of the amount of salt appropriate to the various commercial grades, that could be expected from a given salting operation is calculated. A method for determining an overall transfer coefficient is suggested and a coefficient for the case in point calculated. A regression line for water and salt contents of the fish during pickle salting is given.

INTRODUCTION

SALTING preserves cod by restriction of bacterial and enzymic activity, and is usually followed by a period of drying. Many degrees of salting are practised, and before drying the fish may contain from 4 to 20% of salt by weight, depending on the particular cure desired. In general two major categories of salting exist, those of heavy and light salting. In the case of heavy salting, the salt content of the fish is not critical, as long as sufficient salt is present. Light salting is, however, a much more demanding procedure. Within this category several grades of fish exist. Each grade has associated with it a definite range of salt content. The higher the salt content, the less is its market value as a light-salted fish. Thus, in the preparation of top-quality fish, the producer is faced with the necessity of salting between relatively narrow limits, determined by the possibility of spoilage due to an insufficiency of salt, and by downgrading due to an excess. Although copious data are available on the principles of heavy salting of cod (Beatty and Fougère, 1957; McPhail, 1957), fewer data are available concerning the light salting of cod (Beatty and Fougère, 1957; van Klaveren and Legendre, 1958; Legendre, 1960). It is the object of this paper to study a typical light-salting operation in order that ideas and standards of comparison might be afforded for the evolution and evaluation of possible improvements on the current light-salting procedure.

The chemistry of fish salting is a complex topic, a detailed discussion of which lies outside the ambit of this paper. It is, however, desirable to review certain general technological ideas, and to develop some basis for comparison of data obtained under different conditions.

When a portion of cod muscle is placed in a salt environment, whether dry

¹Received for publication August 6, 1959.

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or in aqueous solution, it immediately tends to equilibrate with its surroundings. This equilibrium may be partly defined for practical purposes as an approximate equality of the brine in the fish (i.e. the amount of salt in the fish expressed as a fraction of the total salt and water in the fish) to that of the ambient brine (Reay, 1936; Jarvis, 1950, p. 39; Fougère, 1952). To complete this description of the system at equilibrium, it is necessary to establish the ratio of this internal brine to muscle, and hence the ratios of salt and water to muscle. These can vary in a complicated manner depending on the method of application of salt or concentration of ambient brine, due to a change, broadly referred to as denaturation, in a protein fraction of the muscle known as actomyosin (Duerr and Dyer, 1952). The latter constitutes some 75% of the total protein present in the muscle. Many factors can affect the denaturation process, notably salt concentration, pH, and temperature. Although the water-retention capacity of the fish protein can vary markedly in dilute brines and for low internal salt concentrations, a critical internal salt content exists in the region of 8% (percentage salt on wet basis), above which the protein is denatured rapidly and salt gain is accompanied by water loss. In commercial practice, dry salt is usually employed. The lightest degree of fish salting involves the addition of an amount of dry salt sufficient to ensure denaturation if the system is allowed to come to equilibrium.

Throughout the course of a dry-salting operation, the average water concentration in a fish inversely follows its average salt concentration. The rate of salt uptake is in constant ratio to the rate of water loss. This would seem to hold even if only a small quantity of salt is taken up by the fish. The implication is that salt and water exchange is largely confined to the region of denatured muscle. Thus we have a picture of a "front" at which denaturation occurs, moving into the muscle. Ahead of this "front", the salt penetration is relatively insignificant; behind it, the bulk of the salt and water exchange takes place. Such evidence is afforded by curves showing the average salt content of a thick fish, and the salt content of its central region, as functions of time (Dyer, 1942; Duerr and Dyer, 1952). During the first day a very marked difference in slope is apparent between the two curves. The average salt content of a light-salted fish may be as low as 4%. It is important to note that most of this salt is in a denatured region extending inward from the surface. It is obvious that the question of denaturation rate is of considerable importance in deciding the overall speed at which salting occurs. Available data indicate that denaturation occurs rapidly as soon as sufficient salt is present, and that temperature has no noticeable effect on this rate in the ordinary range of salting temperatures, say 32 to 60°F (0 to 16°C) (Duerr and Dyer, 1952).

Some retardation in the rate of penetration of salt occurs in the lower part of this temperature range. Few data are available on the effect of pH in the present context. In the work described in this paper control of pH was not attempted. Throughout the greater part of the salting time the pH value lay in the range 6.5 to 7.0. Conditions were similar to those under which the above denaturation work was carried out and also to those described by Castell (1953) in work on storing of light-salt cod in its own brine.

In the present discussion, the term "salt" is assumed synonymous with sodium chloride. The experimental work described below was based on the commercial Turks Island salt commonly employed in the industry. On the average this salt usually contains some 4% of impurities, primarily salts of calcium and magnesium (Hess, 1942). These tend to retard the penetration of sodium chloride (Tressler, 1919). It is unlikely that significant differences will result in comparison with other solar salts which tend to be similar with respect to contamination. Some significant discrepancy would probably be encountered in comparison with results of employing pure sodium chloride.

The data of Reay (1936) and Dyer (1942) indicate an exponential approach to equilibrium of the fish brine concentration with the ambient brine that forms during salting. For a great part of the overall salting period the fractional approach to equilibrium appears to be the same whether a light- or heavy-salting operation is being carried out. It seems reasonable, for practical purposes, that throughout a considerable part of the salting time the driving force during salting might be taken as the difference in concentration between the average internal fish brine and the ambient brine. If the extent of the latter is sufficient to remain virtually unchanged in concentration throughout salting, the resulting situation is analogous to "Newton's Law of Cooling". In the case of light salting, where a limited quantity of dry salt is employed, the picture is more complicated, since the concentration of the ambient brine formed changes not only through salt and water exchanges with the fish, but also as more of the undissolved salt goes into solution.

By the following method the overall transfer coefficient characterizing the resistance to salting under a given set of circumstances may be calculated. This affords a convenient means of comparison for the effects resulting from changes in the operating variables. The fundamental rate equation may be stated as follows:

$$\frac{dC_f}{dt} = K(C_b - C_f)$$

where C_b and C_f are respectively the ambient and fish brine concentrations, and K is the overall transfer coefficient. Integration of this equation, and its solution over a particular time interval, as indicated by the subscripts 1 and 2 to t , yields the following expression:

$$K = \frac{\log_e \frac{C_{f2}}{C_{f1}}}{\int_{t_1}^{t_2} \frac{C_b}{C_f} dt - (t_2 - t_1)}$$

It is convenient to solve the integral in the denominator graphically. This may readily be done since experimental values of C_b and C_f at particular times may be determined and it is only necessary to plot the ratio as a function of time and apply Simpson's rule. (K actually varies with time. Integration produces

an overall mean value. Theoretically it is possible to examine the variations of K with time by measuring slopes at different points. This is unsatisfactory unless a large number of points are available to define the curve and the slopes accurately.) Values of this coefficient for the particular case in hand were worked out and are presented later.

EXPERIMENTAL METHODS

The investigation was carried out by observing the changes in salt uptake by post-rigor fish at different levels in salting tanks left undisturbed at constant temperature for various periods of time. All the fish used were caught by an off-shore longliner and were gutted at sea. Salting was carried out within 24 hours of death. In the experiments, split fish weighing $1\frac{1}{2}$ to $2\frac{1}{2}$ lb (0.7 to 1.1 kg) were placed in aluminum tanks 4 feet wide, 4 feet long and 3 feet deep ($1.2 \times 1.2 \times 0.9$ m), each layer being salted by weight, using 10 lb (4.5 kg) Turks Island salt to every 100 lb (45 kg) of fish. The actual salting operation occupied some 2 hours, the brine forming rapidly and reaching the top layers of fish within a further period of about 2 hours. The total weight of fish in each tank was usually of the order of 2700 lb (1200 kg). During the salting operation, sets of ten tagged samples were distributed in regular pattern at each of seven different layers in the tank. Tubes were placed on top of each of these layers so that brine samples could be withdrawn for testing. These also afforded an approximate means of checking temperatures throughout the tank. A wooden rack loaded with weights was used to keep the upper layer of fish immersed after formation of the brine. The experiments took place in constant-temperature rooms at 42°F (5.6°C) and 58°F (14.4°C). When necessary the fish were spread for a short time to come to room temperature before being placed in the tanks.

Moisture contents were determined by drying representative samples of the muscle from a given fish for 24 hours at 221°F (105°C). Salt contents were estimated by determining the electrical conductivity of an aqueous extract of the dried residue remaining after the moisture determination. The salt value obtained from a predetermined calibration curve was then corrected for a blank value for unsalted fish muscle. The blank value was based on estimates on fifty fish of varying post-mortem times and history, and as determined in this manner had a value equivalent to a salt content of 0.8%. The standard deviation proved less than 0.07% and was deemed insufficient to invalidate the method in its present context.

RESULTS

VARIATION OF SALT PENETRATION WITH DEPTH

After various periods of immersion in the tank at 42°F, marked differences in salt uptake were noted between the top, bottom, and central regions. This is illustrated in Fig. 1 where layer 1 represents the top, and layer 7 the bottom layer of fish in the tank. Each point represents the average value of salt content for ten fish from a given layer. The significance of these results is shown by the

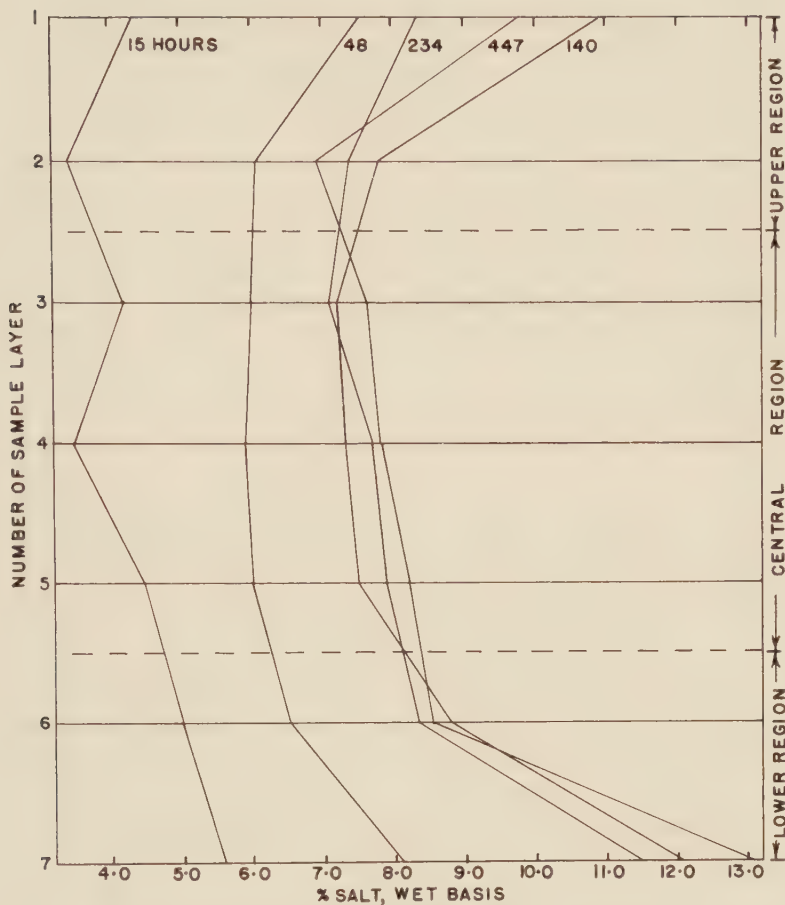


FIG. 1. Mean salt penetration into fish at different levels in a salting tank after various periods of salting.

fact that a standard error of the mean calculated from the greatest standard deviation encountered in any of these sets of ten samples from a given layer was 0.4%, a figure considerably less than the general differences existing between the different regions of the tank. The mean salt content of the fish from different layers tended to show high values in both upper and lower regions.

Though a higher salt concentration at the bottom of the tank might well be expected, the fact that a similar condition occurred at the top is not so readily explicable. Above the surface layers of fish, which were kept immersed by a rack and weights, there existed a few inches of free brine. It was probably the building up and existence of this reserve of adjacent brine which permitted the upper layers to attain initially higher salt contents.

A similar pattern was observed at 58°F although a shorter series of immersion periods was occasioned by more rapid spoilage of the fish.

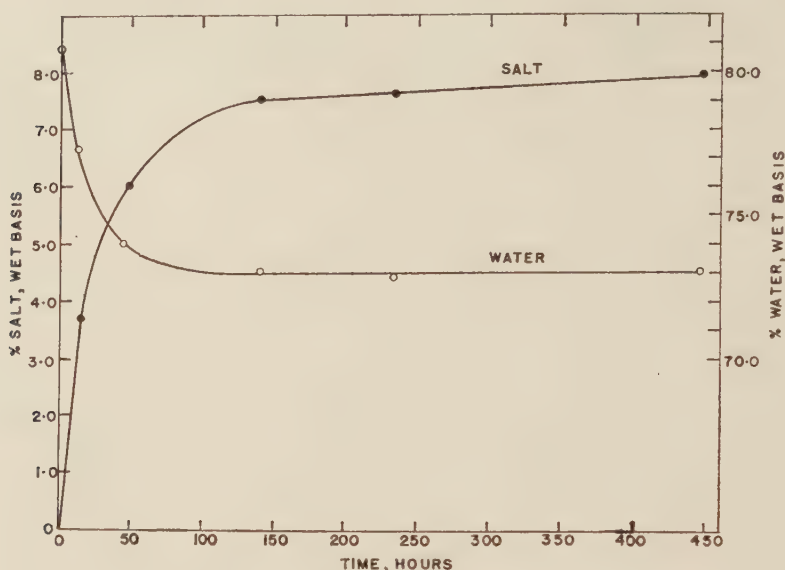


FIG. 2. Variation of salt uptake and water loss for the bulk of fish in the central region of the tank at 42°F.

MEAN RATE OF SALT UPTAKE FOR THE CENTRAL REGION OF THE TANK

The similarity of values observed for layers 3, 4 and 5 led to their being plotted as a single average in Fig. 2, showing the overall uptake of salt and loss of water for the central bulk of the fish. The standard deviation for a series of samples placed in a given layer was close to that obtained when a single average value for the three central layers of samples was employed. After 6 days, the bulk of the salt and water transfer had taken place. For split fish of similar size, placed in an excess of dry salt, Dyer (1942) has shown that about the same time is required to reach a like degree of approach to equilibrium.

CHANGES IN BRINE CONCENTRATION

In most experiments, records of brine concentrations were maintained. In Fig. 3, curve A shows the variation with time of the mean value of brine concentration for the upper six levels in the tank. These values differed little from layer to layer. Curve B refers to the brine concentration immediately above the bottom layer of fish. These curves are typical of the general behaviour of the brine in the tanks. For the first 2 days, the bottom layer shows something of an increase, commencing then to diminish at a rate similar to that in the rest of the tank. When comparing the rates of change in Fig. 2 and 3 it is well to bear in mind that the ratio of brine to fish in the tank was of the order of 1:3 and that small concentration changes in the fish reflect larger changes in the brine. It is apparent that the curve for the brine concentration in the bulk of the tank is approaching the region of 12 to 13%. This agrees with the final overall brine concentration in the system predicted by consideration of the total salt and water

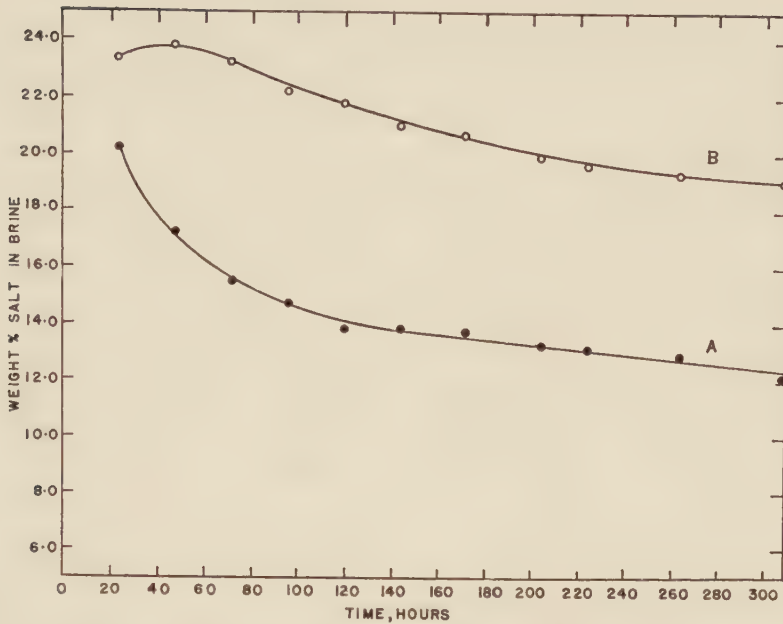


FIG. 3. Curves showing the mean value of brine concentration for A, the six upper levels, and B, the lowest level.

in the system and equality of internal fish and ambient brines at equilibrium. Direct measurement was also made of this quantity by weighing the total brine formed in an experiment, mixing it and observing its concentration. The result was in agreement with that expected.

After a period of about 300 hours, the brine concentrations throughout the tank became prone to a disturbance affecting all levels. The cumbersome nature of the experiments and limited practical significance did not warrant a close examination of this phenomenon. It was probably associated with the major pH change which occurs when fish are held under pickle for lengthy periods of time (Castell, 1953).

SALT TRANSFER COEFFICIENT

Using the equation described above, salt transfer coefficients were calculated for the common range of commercial light-salting time, which is usually about 48 hours. These values are given in Table I. The coefficients are based on the

TABLE I. Overall transfer coefficients for a single fish, as calculated for the experiments at 42°F.

Period	Coefficient
<i>hours</i>	
10 to 20	6.4×10^{-3}
20 to 30	6.9×10^{-3}
30 to 40	6.1×10^{-3}
40 to 50	6.2×10^{-3}

data of Fig. 2 and 3, and are applicable to a single fish from the central region of the tanks. Unfortunately sufficient data were not available to determine similar coefficients for the use of salting at 58°F.

EFFECT OF TEMPERATURE

A number of experiments were carried out at 58°F but this higher temperature was found to have relatively little effect on the rate of uptake of salt. It was noted that in general the uptake of salt by fish in the upper and lower regions was about 1 to 2% higher, and in the central region about 1 to 2% lower, than for the corresponding time at 42°F. Corresponding changes occurred in the brine, the concentrations at the bottom being a little higher, and in the central region of the tank a little lower, than in the experiments at the lower temperature. Due to the problem of spoilage, it was not desirable to continue experiments for longer salting periods.

EFFECT OF FINE SALT

In one experiment at 42°F, finely ground Turks Island salt was used rather than the coarse salt employed in the other experiments. This yielded no clearly discernible improvement on the variability of salt uptake observed in experiments with coarse salt. A marked effect was observed, however, in that the disparity between the salt uptake of the central region and that of the lower regions was greatly reduced. High values were still obtained in the upper region of the tank. The salt uptake for the central region was consistent with that which would have been predicted for coarse salt as taken from Fig. 2. Thus, grain size of salt in dry salting would seem to have little effect on the rate of salt uptake. This is consistent with Bitting's (1911) observations.

EFFECT OF DEPTH

In general the experiments were carried out using depths of fish slightly under 3 feet (1 m). One experiment was carried out in which the depth of fish was 18 inches (0.5 m). The same discrepancy was observed as in the case of the greater depths of fish: excessive salt penetration took place in the upper and lower regions as compared with the central region.

SALT AND WATER REGRESSION EQUATIONS

It is apparent from Fig. 2 that the water and salt transfer are in a close inverse ratio. On a basis of analyses for salt and water on representative samples from each of 860 fish immediately following removal from the salting tanks, the following regression equations were calculated, yielding a correlation coefficient of 0.93:

$$\begin{aligned} S &= 61.12 - 0.74M \text{ (standard error of estimate} = 0.7) \\ M &= 81.83 - 1.19S \text{ (standard error of estimate} = 0.9), \end{aligned}$$

where S and M are respectively the percentage of salt and moisture expressed on a basis of wet weight. Similar correlations with different constants result if a

dry, salt-free basis is employed. The line showing the estimated amount of salt associated with a given water content, with confidence limits at 80 and 95%, is given in Fig. 4. Points A to E, corresponding with the average water and salt

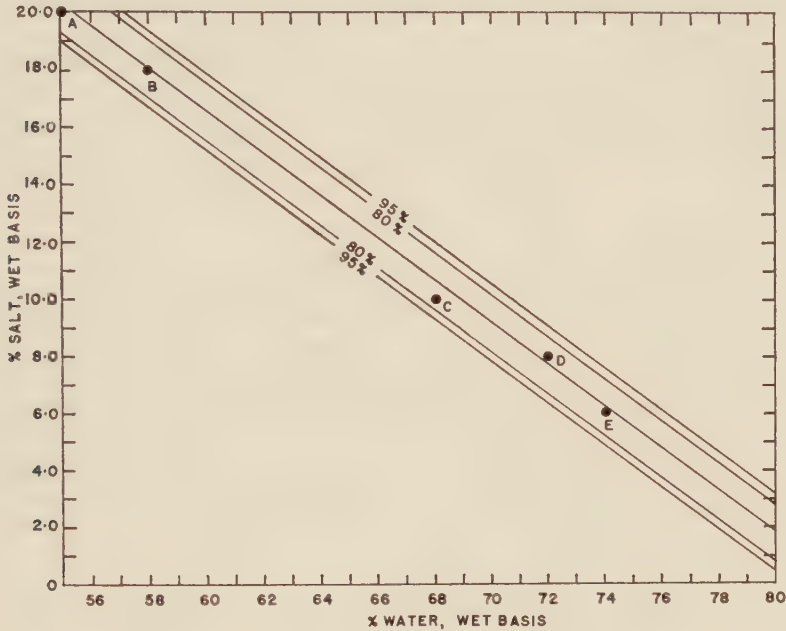


FIG. 4. Regression line of salt on water with confidence limits at 80 and 95% with points corresponding to the average accepted salt and water contents of Canadian salt cod products as follows: A, kenched heavy-salt fish; B, pickled heavy-salt fish; C, Newfoundland kenched light-salt fish; D, fall Gaspé cure; E, Gaspé cure.

contents of the various categories of salted fish produced in Eastern Canada, as reported by van Klaveren and Legendre (1958), demonstrate conformity of the line with general experience. The water content of fresh cod, as predicted by the intersection of the line with the appropriate axis, is 83%. This is somewhat higher than the usually accepted water-content value of about 81%, although the latter is subject to a good deal of uncertainty. In the case of four samples of fresh cod, for instance, Shewan (1944) has reported values ranging from 81 to 84%.

It is of interest to note that the only difference in respect to final water content between kenched cod and pickle-salted cod is that the former tends to have a slightly lower content. This is readily explicable in terms of evaporative losses.

An important aspect of this regression relation lies in the fact that, provided the fish are allowed to come to equilibrium with the salt environment, the average salt content of the fish may be predicted with reasonable accuracy for any of the amounts of salt usually employed in commercial operations.

VARIATION IN SALT CONTENT AMONG SAMPLES FROM CENTRAL REGION OF TANK

The amount of variation of samples withdrawn from the central region of the tank is a useful index of the degree of uniformity of product that may be obtained in this method of salting. Table II shows the mean values of salt

TABLE II. Mean values of salt content for three central layers with their standard deviations and confidence limits for experiments at 42°F.

Brining time in hours:	15	48	140	234	441
	<i>percent salt in fish from central layers</i>				
Mean value	3.7	6.0	7.5	7.5	7.9
Standard deviation	0.7	0.6	1.1	0.8	1.2
80% of the fish lie between	2.5 - 4.9	5.1 - 6.9	5.8 - 9.2	6.3 - 8.7	6.0 - 9.8
95% of the fish lie between	2.3 - 5.1	4.8 - 7.2	5.4 - 9.6	5.9 - 9.1	5.5 - 10.3

content for the three central layers of samples which were used to plot Fig. 2, together with corresponding standard deviations and confidence limits at 80 and 95%.

No trend with time or increased temperature toward greater uniformity of salting could be observed. Similar standard deviations were noted for upper and lower regions of the tank.

It is of interest to compare these values with the ranges of salt content normally associated with the commercial grades of fish in Newfoundland. These latter are usually expressed on a basis of dry weight. If, however, the amount of moisture associated with the given salt content of a fish be obtained from the correlation referred to above, we may express these weights in terms of the salt contents on a wet basis at the completion of salting, on the assumption that the water loss is due solely to the action of the salt. These data are listed in Table III.

TABLE III. Relation between salt content on dry and wet basis at the end of salting.

Grade	Salt content	
	Dry basis	Wet basis
	%	%
Choice	18 - 21	4.0 - 5.0
Prime	21 - 24	5.0 - 6.0
Madeira	24 - 28	6.0 - 7.6
Thirds	28 - 31	7.6 - 9.1

From Fig. 2 it is seen that after a period of 24 hours, the mean salt concentration of the fish in the central region of the tank should have attained 4.6%. If the standard deviation is assumed to be 0.7%, as seems reasonable from Table II, then we may expect that 48% of the fish in the central region will achieve

Choice grade. If, on the other hand, we leave the fish in the tank for 35 hours, 83% of the fish in the central region will be within the top two grades, Choice and Prime. These percentages are based on the mean and limiting values of salt concentration, for the grades Choice and Prime as shown in Table III. Assuming a normal distribution and the appropriate standard deviations as obtained from Table II, the proportions of fish within the specified limits are easily calculated with the aid of a probability table. On the basis of the data available, estimation of the grades of fish in the top or bottom regions of the tank is somewhat speculative, but after a period of some 35 hours the fish in these regions, comprising about 50% of the total fish, should be primarily in the grades Madeira or Thirds.

DISCUSSION

The main problem confronting the salt fish producer is to salt fish within relatively narrow tolerances. The difficulties involved in doing this on a commercial scale are abundantly illustrated by the above data, based on experiments in which salting was carried out by careful proportioning of salt to fish of selected weight, the fish all being in good condition. The best result that could be anticipated, assuming that 50% of the total fish is in the central region, is about 40% in the top two grades. It is useful to compare this with Newfoundland light-salt fish production in general. Table IV shows the proportions of light-salt cod in

TABLE IV. Percentages of light salted exports by grade.

Grade	Newfoundland exports		Bonavista exports	
	1954	1955	1954	1955
	%	%	%	%
Choice	1.5	3.7	7.4	9.6
Prime	2.8	6.8	28.2	30.2
Madeira	49.2	51.4	34.8	33.5
Thirds	35.2	26.0	24.2	21.4

the two top grades produced during the years 1954 and 1955. For purposes of comparison values are also given for the Bonavista Experimental Plant (Conboy, 1957). It is interesting to note the agreement of the above-mentioned value of 40% with the corresponding 1955 value of 39.8% for Bonavista. The excellence of this agreement is to some extent fortuitous since no account has been taken of differences in production procedures. At Bonavista, the variation of fish size and downgrading due to faulty splitting may have been offset by the fact that the tanks used there were 2 feet deeper than those employed in the present work.

The biggest factor affecting the uniformity of salt uptake is that of fish surface area available for salt transfer. Schmidt (1952) has observed in the case of brined herring that variation in salt uptake cannot be explained in terms of fish thickness and fat content. Thus for improvement in the yield of top-quality fish, a very desirable factor is increase in the area of the fish surface

accessible to the brine. Circulation of saturated brine instead of dry salting would afford an excellent means of control of salt uptake and also, by passing the brines through a heat exchanger, of temperature. This is an important factor in summer conditions. The question is one, however, to be answered on economic grounds. Less elaborate and more in line with current practice, the use of deeper tanks, finer salt, or an arbitrary distribution of salt, are worth investigating. It is of particular interest that uniformity of salting cannot be increased by prolonging the salting time.

Of some assistance is the idea of a constant fractional approach to equilibrium independent of the amount of added salt. The salt content of the fish at equilibrium may easily be estimated from the assumption of equality of brine concentrations, the water and salt regression relation, and the overall water and salt content of the system. Thus, for example, if the salt content of heavy-salt fish at equilibrium is assumed to be 20%, and that of the light-salt fish prepared under the conditions described in this paper is 12%, after 24 hours some 50% of the total transfer will have occurred, the salt content in the first case being about 10% and in the second 6%. This may be seen by comparing Fig. 2 with the curve published by Dyer (1942) for heavy salting of fish of about the same size. More data are, however, desirable.

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The Partial Desalting of Salted Cod¹

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ABSTRACT

The results of small-scale experiments on the desalting of heavy-salted cod are presented. A method is proposed for a commercial desalting operation.

INTRODUCTION

INTEREST has been shown in utilizing the better keeping qualities of heavy-salt bulk cod as compared to light-salt cod, and a desalting process prior to drying, as aids to light-salt fish production where circumstances render prompt drying of the fish difficult. This is a problem of some complexity. Any general practical solution requires a large number of possible initial salt and water contents of the heavy-salt bulk to be considered in setting up the desalting procedure. It is also important that the fish at the end of desalting shall be reasonably uniform in salt content. Complete desalting of the surface is conducive to ready spoilage.

Two possible desalting methods are feasible. The first method involves brief periods of immersion of the heavy-salt bulk in fresh water, followed by periods of press-piling to permit diffusion of salt in the muscle to the salt-depleted region. This is laborious and involves substantial risk of spoilage. The second method constitutes a considerable improvement and entails immersing the heavy-salt bulk in a limited quantity of fresh water, and allowing the whole to come to equilibrium. This method will be elaborated below.

EXPERIMENTAL

In the present work, a series of experiments was carried out to determine the general characteristics of a desalting procedure. Rectangular blocks of muscle were cut from heavily salted cod obtained from a commercial producer. The water and salt contents were determined on samples removed from parts of the fish adjacent to the block. The water was determined by drying to constant weight at 105°C. Salt was measured by potentiometric titration using a glass-silver/silver chloride electrode pair. The block was suspended by means of a wire stirrup in a vertical tared cylinder containing a quantity of water. At intervals throughout the experiment the block and the cylinder were each weighed and a small aliquot of ambient solution was removed for salt analysis. This enabled the water and salt exchanges to be readily followed. Agitation was carried out in different rooms, each at a controlled temperature. The results of this work are summarized in Table I.

On the basis of the results obtained from these experiments the work was repeated on a larger scale using 50-lb batches of fish. These were placed in a shallow tank, the desalting water being slowly circulated by means of a pump

¹Received in revised form for publication May 30, 1961.

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from one end to the other. Closed-circuit pumping of this nature allied to summer conditions engendered a temperature increase sufficient to reduce the first batch of fish to an unpleasant paste. Thus a modest degree of cooling was incorporated in further experiments by means of a small refrigeration unit and cooling coils immersed at either end of the tank to prevent the temperature rising beyond the critical region of about 80°F. To ensure adequate circulation of water between the fish, longitudinal wooden slats, of 1- by $\frac{1}{2}$ -inch cross-section were used to space the consecutive layers.

The rate of desalting is primarily dependent on the volume of desalting water, temperature, agitation, and fish size. The results of a series of experiments in connection with these factors, using standard sized blocks of fish muscle, are shown in Table I. These results have been expressed in terms of the numbers of hours to reduce the salt content of the fish to 8, 6, and 4% respectively. Although the experiments were carried out on a small scale, they were found to constitute a useful basis for estimating the performance of large-scale systems involving batches of split fish. Although shorter desalting times result from the use of a large water volume, the advantage is not so great but that it is readily offset by the more uniform final salt distribution associated with an equilibrium process. The effect of temperature is marked, a drop from 75 to 37°F approximately doubling the time required for the same degree of desalting. Agitation can decrease desalting time but hardly to a degree that would warrant elaborate equipment.

RESULTS

When fish are placed in dry salt and allowed to come to equilibrium in their own pickle, it is found that the concentration of brine in the fish (i.e. the salt in the fish expressed as a fraction of their total salt and water content) effectively equals the concentration of the brine surrounding them (Fougère, 1952; Reay, 1936). It has also been found that the salt taken up by the fish at any time during the salting is in simple proportion to the amount of water lost (Crean, 1961). Thus if the percentage of salt in a fish at any time during salting is plotted against the corresponding percentage of water, the points will be on a straight line. It was found in the present work on desalting that a similar type of behaviour is encountered, the water and salt exchange being in simple proportion and proceeding to an eventual equality of brine concentration throughout the system.

DESALTING METHOD

We now have the means to postulate a simple method for a commercial desalting procedure. Consider Fig. 1. The right-hand scale states the quantity of dry salt to be added to 100 lb of fresh fish which, when allowed to equilibrate in its own pickle, will give a salt content on a wet basis exactly opposite on the left-hand scale. Consider then a batch of fish with water and salt contents depicted by the co-ordinates of point A. Prolonged storage will result in moisture loss and increase of the percentage wet weight of salt in the fish. During storage, the water and salt contents will progress along AB. Suppose the batch is weighed and found to have lost 25% of the weight it originally had at A. This

TABLE I. Summary of the effects of different variables on partial desalting

Primary variable	Temp.	Initial block dimensions	Salt and water content (on wet basis)						Volume of desalting water	Degree of agitation *	Desalting time to attain salt content of			Slope of desalting line
			Initial state		After 24 hr						8% hours	6% hours	4% hours	
			Salt	Water	Salt	Water	Salt	Water						
Volume of desalting water	75	2 × 2 × 10	16.9	49.8	1.1	72.7	3000	Mild	3.0	5.5	9.0	0.69		
	75	2 × 2 × 10	16.9	52.2	3.0	73.5	195	Mild	3.1	6.0	12.2	0.62		
	75	2 × 2 × 10	17.0	51.6	4.7	73.3	100	Mild	3.6	8.1	...	0.65		
Temp. effect (small volume of desalting water)	37	2 × 2 × 10	16.2	49.8	4.9	69.8	136	Mild	6.7	13.3	...	0.61		
	75	2 × 2 × 10	16.2	49.8	3.6	70.3	136	Mild	3.1	6.2	15.5	0.61		
	37	2 × 2 × 10	17.0	51.6	5.6	73.1	100	Mild	6.4	15.7	...	0.63		
Block size (small volume)	75	2 × 2 × 10	17.0	51.6	4.7	73.3	100	Mild	3.7	8.2	...	0.65		
	75	2 × 2 × 10	16.9	52.2	3.0	73.5	195	Mild	3.1	6.0	12.2	0.63		
	75	3 × 3 × 10	16.9	52.2	4.0	71.8	365	Mild	5.8	11.0	23.5	0.63		
Agitation (small volume)	75	2 × 2 × 10	16.2	49.8	4.0	70.0	136	Mild	3.1	6.2	20.0	0.63		
	75	2 × 2 × 10	16.2	49.8	3.6	70.3	136	Strong	3.7	7.5	14.2	0.61		

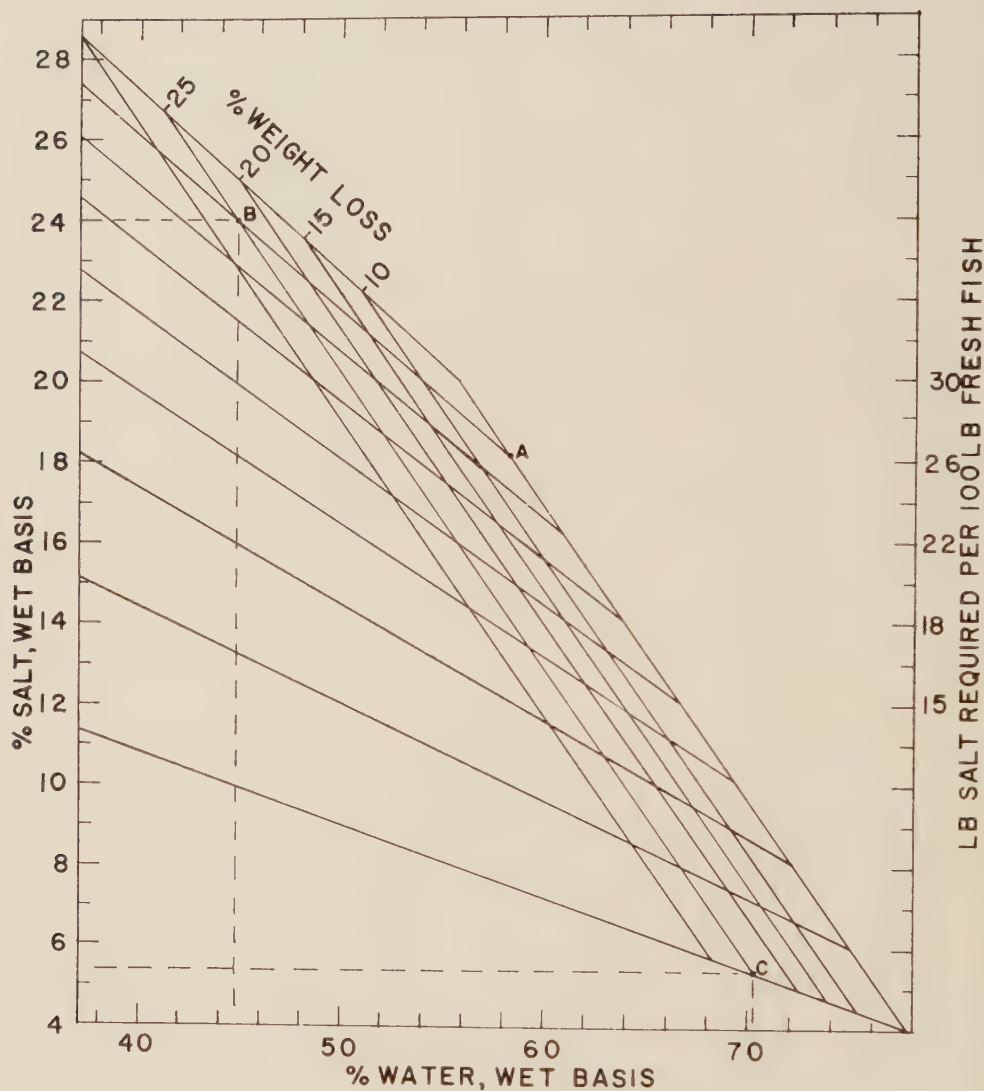


FIG. 1. State diagram for salting and desalting of fish muscle.

locates point B. Consider for example, 100 lb of fish containing 24% of salt and 44.8% water. This corresponds to point B. Suppose it is desired to reduce the salt content of this fish to 5.4% with a water content of 70.3%. This corresponds to point C. The required amount of water may be estimated by means of the nomograph in Fig. 2, where scales X and Y are respectively the initial percentage salt and water contents of the fish, and scales X' and Y' are respectively the final salt and water contents when the system has come to equilibrium. The nomograph is used in the following manner. Draw a straight line through the

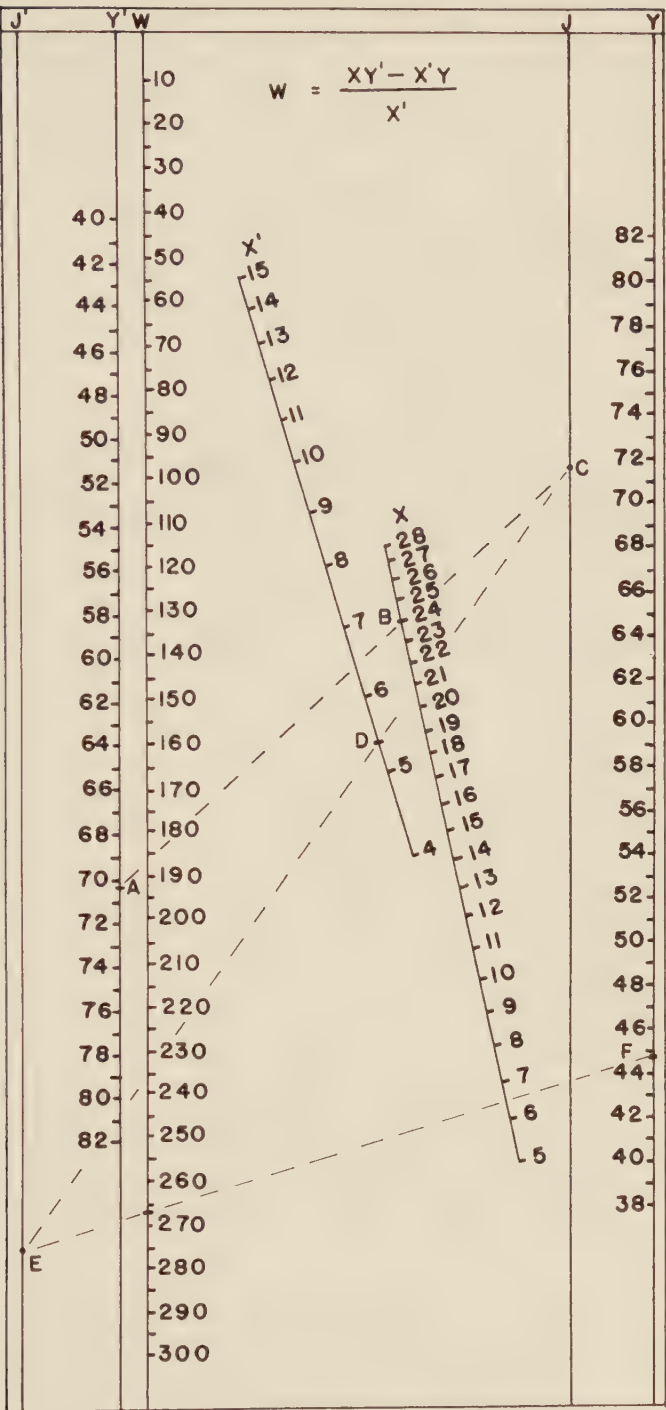


FIG. 2. Desalting nomogram.

points A (70.3 on Y') and B (24.0 on X), and extend it to intersect the line J at C. From point C draw a straight line to point D (5.4 on X'), and extend it to intersect the line J' at E. Join E to the point F (44.8 on the scale Y). The intersection of the line EF with the scale W gives the amount of water, 267 lb, to be added.

DISCUSSION

To test the efficacy of the method, some experiments were carried out on 50-lb batches of heavy-salted cod. The results proved satisfactory. Thus for example, salt analyses of six fish removed from a batch which was calculated to have a final salt content of 5.0% were: 5.0, 5.1, 5.0, 5.0, 5.0, 5.2%. Elaboration of this larger-scale work to include factors affecting rate was not undertaken at this time.

In setting up a commercial-scale desalting operation, one of the major difficulties is that of separating the layers of fish. Many methods might be tried, as dictated by the costs involved. In experiments carried out at this Station longitudinal wooden battens of $\frac{1}{2}$ -inch thickness when placed between adjacent layers were found effective. This permits a ready flow of water down the tank between the layers of fish.

It sometimes happens that the desalting water added is insufficient to cover the fish. In this case the calculated amount of desalting water should be added, followed by a quantity of brine of strength the same as that anticipated when the system has come to equilibrium, sufficient to cover the fish.

With respect to agitation, the principal factor is to avoid the accumulation of a strong brine in the lower region of the desalting tank. If a simple recirculatory pumping system is employed, it is important to remember that continuous operation may lead to a rise in temperature sufficient to ruin the fish. Piping connections on the suction side of the pump must be tight, and the suction inlet well submerged, or excessive foaming will result.

In carrying out a desalting operation, measurements of the specific gravity of the desalting water afford a simple means of determining the degree of approach to equilibrium. Dissolved protein was not found to affect these measurements to a significant degree. Once the specific gravity of the desalting water becomes reasonably constant, the fish may be removed for drying.

The procedure outlined above is believed to afford a rational basis for the setting up of a salting-desalting process. The salt concentrations to be employed will be largely determined by the storage conditions available and the type of product required. It is recommended that operators setting up a process pay particular attention to the specific gravities of the desalting water as an index of the degree of completion. Thus a regular routine may be set up on an empirical basis for any given set of conditions.

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Chemical Characteristics of Salted Cod¹

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ABSTRACT

A study has been made of the formation of decomposition products in three different types of salted codfish. The total volatile acids, trimethylamine, ammonia and free α -amino acids were determined on 50 samples of each type of salted fish. The total volatile acids and trimethylamine were found to be chemical indices which enable a clear differentiation between light- and heavy-salted cures. The presence of large quantities of these two decomposition products is typical of light-salted cures, especially of the "Gaspé cure".

The influence of the degree of salt saturation in the brine and in the muscle itself during processing, on formation of decomposition products, is discussed.

INTRODUCTION

THE TECHNOLOGY of salt curing of codfish has not been studied exhaustively and consequently salted cod has remained a product of frequently uneven quality, sometimes unattractive to the customer, although it is an inexpensive source of protein-rich food. Some of the aspects of processing salted cod were reviewed by Beatty and Fougère (1957) and by van Klaveren and Legendre (1958), and a selected bibliography of salted cod was recorded by McPhail (1957).

This paper forms part of a study on the chemical transformations in the flesh of salted cod during processing. The attempted purpose is to characterize, and to define chemically, a few types of Canadian Atlantic Coast salted cod.

The formation of a number of substances in unsalted cod muscle has been investigated to evaluate the state of spoilage of fish. Recently, it has been shown by Hillig *et al.* (1958), in a comparative study of the chemical indices of decomposition of cod, that (total) volatile acids number, formic and acetic acids, (total) volatile bases, (total) volatile amines, and trimethylamine show the highest degree of correlation with organoleptic judgment, while succinic acid and alcohol show less correlation.

With salted codfish, Bilinski and Fougère (1959) have studied the inhibitory effect of salt on proteolysis of the muscle and deamination of amino acids and formation of trimethylamine. The non-protein nitrogenous constituents were also studied by Freixo (1958) in Portuguese light-salted cod. It has also been

¹Received for publication January 4, 1961.

²Deceased.

noted (Cardin *et al.*, 1958) that there is a substantial degree of formation of free fatty acids during processing of salted codfish but it was found to be the same in two types of cures widely different in salt content, namely the light-salted Gaspé cure and the heavy-salted cure. Preliminary determinations also have shown that the amounts of volatile reducing substances do not vary substantially between the light-salted and heavy-salted cure, while on the contrary the total volatile acids content showed significant differences.

In the present investigation the development of the free α -amino acids, ammonia, trimethylamine and volatile acids were examined for their possibilities of defining and of characterizing three different types of salted codfish.

EXPERIMENTAL

MATERIAL

The three types of salted cod can be briefly described as follows: the "Gaspé cure" is a light-salted fish cured by adding 8 to 10 lb of salt per 100 lb of fresh fish. It is kept in the brine for 3 days then dried in the sun to 38% moisture content. The "Fall cure", which is also considered as a light-salted cure, is processed by adding 10 to 14 lb of salt per 100 lb of fish. It is kept in pickle during 6 days then dried to 43% moisture content. The "heavy-salt" is prepared by adding 35 lb of salt to 100 lb of fish and keeping them in the brine for a period of at least 21 days. It can be dried to 40% moisture content (van Klaveren and Legendre, 1958).

Fifty codfish of each type of cure have been analyzed. The fish were caught in the Gulf of St. Lawrence and processed by the industry. To obtain more uniform sampling, all the fish analyzed were taken from lots classified by fishery inspectors as "Choice grade". The salted fish was skinned and the thick part only of the flesh along the backbone was minced and used directly for analysis.

ANALYTICAL METHODS

All the results were calculated on the dry weight of the flesh, salt excluded. The moisture and salt content determinations were done according to conventional methods. Methods used for the other determinations were as follows:

Total volatile acids (TVA): These were steam distilled into 0.02N NaOH, according to the method of Friedemann (1938) as modified by Sigurdson (1947).

Trimethylamine (TMA) and ammonia: 25 g of heavy-salted cod or 8 g of Gaspé cure or Fall cure were used for the determination. After addition of 200 ml of water, the sample was homogenized for about $1\frac{1}{2}$ minutes in a Waring Blendor fitted with a screw cap. One-ml aliquants of the resulting suspension were used for analysis. Total volatile nitrogen and TMA were estimated by the micro-diffusion technique of Conway and Byrne (1933) as modified by Beatty and Gibbons (1937). Ammonia was calculated from the difference between the total volatile nitrogen and TMA nitrogen.

Total free α -amino acids: The procedure of van Slyke *et al.* (1941) measuring the amount of free α -amino acids by titration of carbon dioxide evolved during the reaction with ninhydrin was slightly modified so that direct determination on salted cod could be possible. A 50-ml instead of 25-ml reaction vessel was used. One gram of material, salt excluded, was employed for the determination and 10 ml of water, 2 g citrate buffer pH 2.5 and 250 mg of ninhydrin were added. The boiling time for the reaction and for the distillation were respectively 10 and 5 minutes. Blank determinations were made on each sample of fish with all the reagents except ninhydrin.

RESULTS AND DISCUSSION

The mean content of salt and decomposition products determined in the three types of cure is given in Table I.

TABLE I. Mean decomposition products and NaCl content for three types of salted codfish. TVA values are expressed in millilitres of 0.01*N* NaOH per gram of fish (dry, NaCl-free weight); TMA, ammonia and free α -amino acids in milligrams nitrogen per gram of dry, NaCl-free fish; NaCl as percentage of dry weight. Between parentheses are the limit values obtained.

Compound	Heavy-salt	Fall cure	Gaspé cure
TVA	1.85	6.49	9.66
TMA	0.31	1.66	1.95
Ammonia	0.88	1.35	1.76
Free α -amino acids	2.01	2.50	2.82
NaCl	35.8 (32.3–41.5)	26.7 (21.0–31.7)	19.6 (16.2–23.9)

It can be seen that the mean value of each decomposition product increases with cure of lower salt content. Moreover the TVA and TMA contents are those which show the greatest differences between the three types of cure. In fact, five times more TVA or TMA occur in light-salted Gaspé cure than in the heavy-salt, while the difference is much smaller for ammonia and even less for α -amino acids. The influence of the salt concentration on the formation of decomposition products will be discussed further, but it can be noted here that the salt content of the fish within the same cure varies widely and that the two light-salted cures have salt contents that overlap considerably. The Fall cure particularly extends from the mean value of the Gaspé cure to the values of heavy-salt.

Figures 1, 2, 3 and 4 show the variation in the content of each decomposition product within each type of cure and equally show the differences between the three types of cure.

In each Figure, on the abscissa the total variation in amount of the decomposition product, for one type of salted cod, is divided into four equal groups and the percentage of samples found in each group can be read on the ordinate.

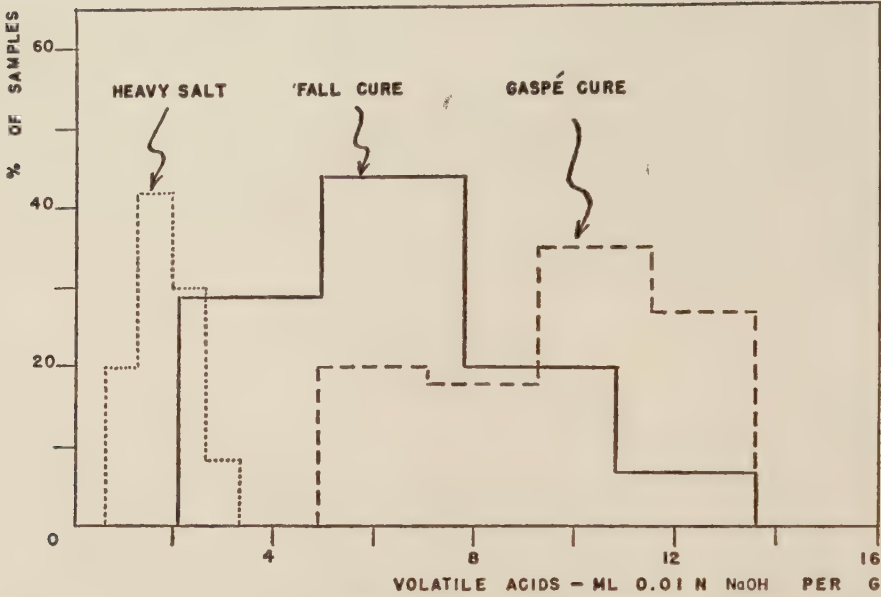


FIG. 1. Distribution of total volatile acids content in three types of salted codfish.

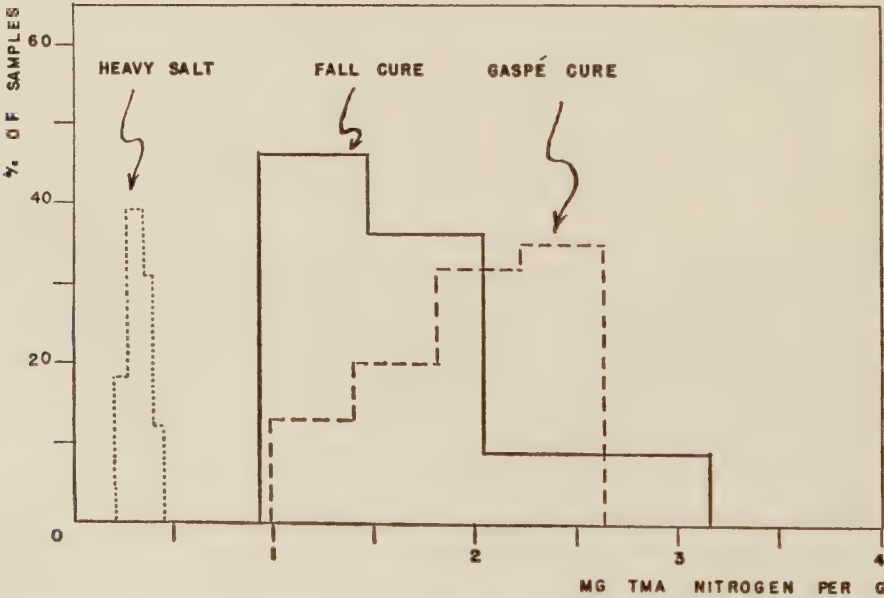


FIG. 2. Distribution of trimethylamine content in three types of salted codfish.

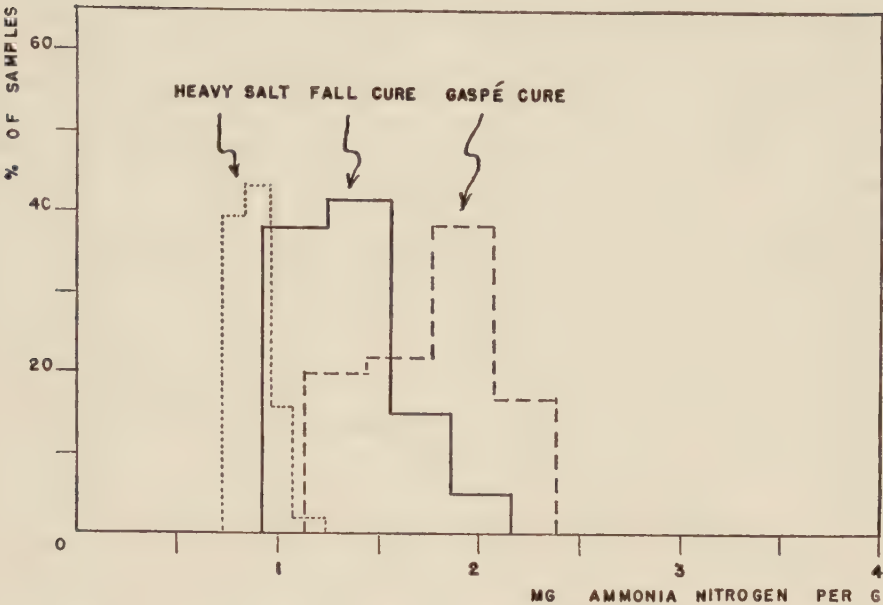


FIG. 3. Distribution of ammonia content in three types of salted codfish.

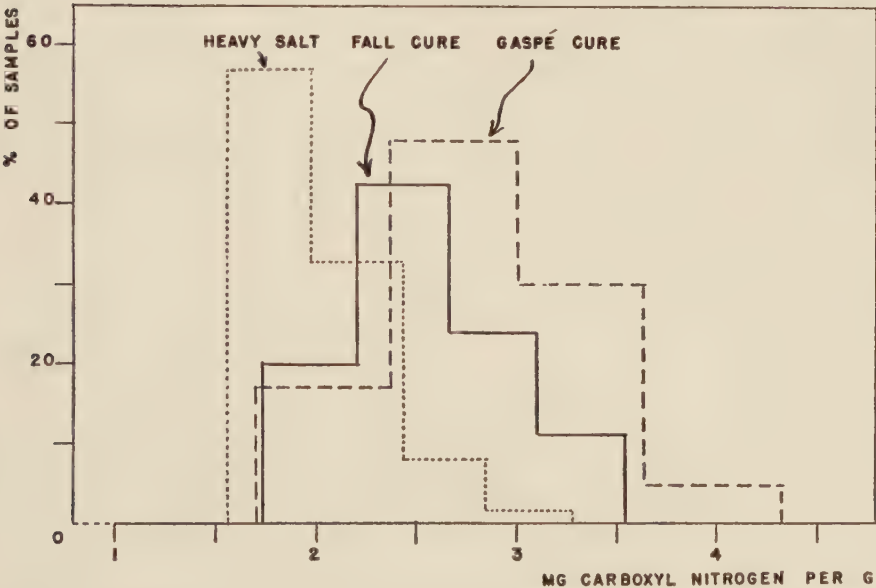


FIG. 4. Distribution of free α -amino acids content in three types of salted codfish.

In Fig. 1, the TVA content is not so widespread in the heavy-salted as in light-salted cures. The distribution of the heavy-salt is clearly separated from that of the Gaspé cure, and the Fall cure occupies an intermediate position. The TMA values (Fig. 2) vary less than the TVA values in the case of heavy-salted cure and are clearly separated from those of both the Gaspé cure and Fall cure. However, in the light-salted cures, the TMA content varies considerably within the same type of cure and the differentiation between the Fall cure and Gaspé cure is less obvious than with the TVA values.

The ammonia content (Fig. 3) is also more homogeneous in the heavy-salted than in the light-salted cures, but the differences already noted between the heavy-salted and light-salted cures are less apparent than for the TVA and TMA. Finally, for the α -amino acids (Fig. 4) there are wide variations within each type of cure even for the heavy-salted cure and, although the mean content in α -amino acids is different for each cure (Table I), it is impossible to see a clear distinction between the different types of salted cod.

The differences observed in the content of decomposition products in light- and heavy-salted codfish must be related with the process of decomposition of the flesh on the one hand and the preservative action of the salt on the other. It is well established with unsalted cod that TMA and TVA contents are indices of decomposition of the flesh (Hillig *et al.*, 1958). On the other hand, the inhibiting action of salt on the formation of TMA in cod has been already noted by Labrie and Gibbons (1937), Winter (1950), Castell and Snow (1951) and Bilinski and Fougère (1959). The formation of quite a large quantity of volatile acids in the Gaspé cure light-salted cod has also been observed by Fougère (personal communication). The present paper, however, brings out the marked difference in TMA and TVA content between commercial types of light-salted and heavy-salted cod. It is apparent that a large formation of TMA and TVA is quite typical of the light-salted cures and especially of the Gaspé cure. The effect of salt on the variation of free amino acids has been studied by Bilinski and Fougère (1959) and it has been observed that a large formation of free amino acids only occurred with small concentrations of salt and when the muscle was well decomposed, and when considerable proteolysis of the muscle has taken place. In the presence of salt, a partial destruction of amino acids with liberation of ammonia could be noticed. With the commercial samples studied in this paper, the quantity of salt added to the fish is sufficient to prevent extensive proteolysis of the flesh and only a limited increase in free amino acids is observed. In a study on Portuguese light-salted cod, Freixo (1958) also found that the amount of decomposition products increases with cures of lower salt content. His data for free amino acids, ammonia and TMA are in the range of those presented in this paper. However the TMA and ammonia content of Portuguese light-salted cures appears to be somewhat lower than that of Gaspé cure and Fall cure.

The better preservation of the flesh from decomposition by employing increasing concentrations of salt can be explained by some observations on the concentration of salt in the flesh of the fish during processing. The concentration

of the brine in the tank, when cod is removed after salting, is 49 to 60% saturated for the light-salted Gaspé-cure, 57 to 78% saturated for the light-salted Fall cure, and 100% saturated for the heavy-salted cure (H. P. Dussault, personal communication). At the same time, the state of saturation of the flesh itself, that is if one takes into account the salt and water content of the flesh, is 86% saturated in the heavy-salted cure, 22 to 35% saturated in the Fall cure and 15 to 22% saturated in the Gaspé cure. Incidentally at this stage of processing, the water content of the flesh is 58% in the heavy-salted cure, 71 to 75% in the Fall cure and 75% in the Gaspé cure. Therefore, whereas the flesh of the heavy-salted cure is continually in the presence of highly concentrated brine which protects the flesh from decomposition, the light-salted fish, while pickling in the brine and even more when it comes out of the brine tank, is highly susceptible to decomposition as the saturation of salt in the flesh is low and its water content is still very high. This might explain the fact that the content of decomposition products is more homogeneous in the heavy-salted than in the light-salted cures. This resemblance in salt saturation between the two light-salted cures might also be the main reason why the content of decomposition products in the dried fish overlaps and is not well separated. Similar observations have been made by Murata and Oishi (1953) who state that "putrefaction in salted fish meat does not occur if the NaCl content becomes 75% of saturated".

It can be concluded from this study that in salted codfish the TMA and TVA contents are chemical indices of decomposition which enable differentiation between light- and heavy-salted cures. The presence of larger quantities of these two decomposition products is typical of light-salted cures, especially Gaspé cure. The ammonia content, and to even less extent the free α -amino acids content, of salted codfish do not show well-marked differences between the light- and heavy-salted cures. The chemical composition of heavy-salted codfish appears to be more homogeneous than the two types of light-salted codfish.

ACKNOWLEDGMENT

The authors wish to express their appreciation to Mr H. P. Dussault of this Station for the use of personal data and for helpful suggestions in the preparation of the manuscript.

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Effect of Estradiol Monobenzoate on some Serum Constituents of Maturing Sockeye Salmon (*Oncorhynchus nerka*)^{1,2}

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ABSTRACT

Blood changes associated with egg production or estrogenization in other egg-laying vertebrates have been obtained in adult sockeye salmon. The blood picture of male salmon following estrogenization approaches that of sexually maturing females. Exogenous estrogen superimposed on endogenous gonadal hormones in maturing female salmon enhances the serum changes associated with egg formation.

INTRODUCTION

IN OVIPAROUS VERTEBRATES each period of egg production is associated with profound changes in blood chemistry of the female. The serum changes, in teleosts [2, 12, 14], in reptiles [8, 14] and in birds [2, 5, 14, 15, 17, 18], include increased concentrations of certain proteins, lipids, vitamins and minerals which are considered to be related to the mobilization of these compounds for egg formation. Several investigators working with teleosts [1, 26], with amphibians [26], with reptiles [8, 26] and with birds [15, 17, 18, 26] have shown that in addition to the normal puberal changes which, as in the mammal, are related to endocrine activity, similar and even greater increases in these serum constituents result from estrogen treatment of egg-laying vertebrates of either sex or of castrates. The study reported here deals with the effect of estradiol monobenzoate on certain serum constituents in adult sockeye salmon, *Oncorhynchus nerka*, during their spawning migration. It forms a part of the study of the physiology and behaviour of salmon outlined by Brett [3].

MATERIALS AND METHODS

Migrating adult sockeye salmon, which were captured at the Great Central Lake dam on the Stamp River near Alberni, British Columbia, were placed in a transportation tank with iced water at 4°C and supplied with excess oxygen. These fish had left the estuary approximately 3 days previously and normally would have spent 3 months in the lake before spawning. The gonads were

¹Received for publication May 5, 1961.

²Paper No. 6 concerning the physiology and behaviour of salmonid fishes, from the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

partially developed at the time of capture, the ovaries corresponding to a rating of 2 on the maturation scale proposed by Davidson and Shostrom [7]. Following transportation to the laboratory at Nanaimo, a distance of 80 miles, 10 fish, 5 of each sex, were arbitrarily placed in each of 2 identical tanks containing 1,100 gallons (5,000 liters) of constantly flowing fresh water.

Twenty-four hours after arrival in the laboratory daily injections of 0.2 mg estradiol monobenzoate in aqueous suspension (B.D.H. oestroform aqueous, 1 mg/ml) were begun on each fish in one tank. At the same time each fish in the second tank received 0.2 ml of the hormone suspending medium (stated by the manufacturers to be "an aqueous solution of a methyl cellulose derivative containing a small percentage of a non-ionic wetting agent"). Hypothermia, 2-4°C, was used as anaesthesia during the injections which were 1¼ inches deep into the epaxial muscles immediately behind the head.

Twenty-four hours after the fourth injection each fish was bled by amputating the tail and the blood was collected in 50 ml plastic centrifuge tubes. Aliquots of whole blood were transferred immediately to heparinized Wintrobe hematocrit tubes and the balance of the blood was allowed to clot at room temperature. The clots were allowed to contract for 2 hours at 5°C after which the serum samples were obtained by centrifuging at 3°C.

Hematocrit values were obtained by centrifuging at 1,700 g and 3°C for 30 minutes; calcium was determined by the method of Clark and Collip [4], and total protein by the biuret reaction [28]. Phosphoprotein phosphorous was determined by Schneider's [21] procedure. The method of Folch *et al.* [10] employing sodium chloride was used to isolate and purify the lipids which were then stored in hexane at -25°C under nitrogen. Total lipid was determined by drying aliquots of the lipid solution at 100°C. Ten volumes of acetone were added to one volume of lipid solution and the phospholipids allowed to precipitate overnight at -25°C; following centrifugation total neutral lipid was determined by drying aliquots of the supernatant at 100°C. Total and free cholesterol were determined by the procedure of Sperry and Webb [24] and esterified cholesterol by difference. King's [13] method was used to determine protein and lipid phosphorus.

Data were subjected to an overall analysis of variance according to Snedecor [23], and values of the average within group standard deviation are tabulated. Tests were made for effects of injections, for differences between sexes, and for interaction between these two.

RESULTS AND DISCUSSION

The experimental results which are summarized in Table I are discussed separately, but throughout the discussion it must be remembered that the fish were not in reproductive rest during the period of this experiment. The experimental fish were already under the influence of endogenous gonadal hormones which probably influenced the response to exogenous estrogen.

TABLE I. Effect of 4 daily injections of estradiol monobenzoate on some serum constituents of maturing sockeye salmon. Data are averages for 5 fish of each sex on each treatment, and the average within-group standard deviation is shown. Samples were taken 24 hours after last injection. LSD = least significant difference between any two groups. * = significant at $P = 0.05$. ** = significant at $P = 0.01$. NS = non-significant ($P > 0.05$).

	Control		Injected		Common standard deviation	LSD		Tests of significance	
	Male	Female	Male	Female		$P = 0.05$	$P = 0.01$	Male vs. female	Control vs. estrogenized action
Estradiol monobenzoate, mg	Nil	Nil	4 X 0.2	4 X 0.2	...	...	...	...	...
Body weight, g	2205	2074	1995	2060	365	...	...	NS	NS
Testes weight, g	16.9	...	16.6	...	8.89	...	...	...	NS
Ovary weight, g	...	93.7	...	94.0	13.7	...	...	...	NS
Testes wt./body wt. X 10 ³	7	...	8	...	...	...	...	...	NS
Ovary wt./body wt. X 10 ³	...	43	...	45	...	...	...	...	NS
Egg diameter, mm	...	2.5	...	2.6	...	...	...	...	NS
Hematocrit value, %	48	47	39	41	2.63	3.5	4.8	NS	**
Calcium, mg/100 ml	11.8	13.1	15.1	17.6	1.13	1.3	1.7	*	NS
Total protein, g/100 ml	4.8	5.1	5.2	6.0	0.41	0.6	0.9	*	NS
Total lipid, g/100 ml	2.4	2.0	4.6	5.0	0.90	1.2	1.6	NS	NS
Neutral lipid, g/100 ml	1.9	1.7	3.9	4.1	0.75	1.0	1.4	NS	NS
Total cholesterol, g/100 ml	0.36	0.24	0.45	0.50	0.09	0.12	0.16	NS	*
Free cholesterol, g/100 ml	0.12	0.09	0.22	0.26	0.04	0.06	0.08	NS	NS
Cholesterol ester, g/100 ml	0.24	0.15	0.23	0.24	0.07	...	...	NS	NS
Protein phosphorus, mg/100 ml	3.0	7.4	8.7	13.5	0.98	1.3	1.8	**	NS
Lipid phosphorus, mg/100 ml	57.0	43.1	81.5	97.4	26.4	35.2	48.7	NS	**

BODY WEIGHT, GONAD WEIGHT AND EGG DIAMETER

There was no significant difference in total body weight between the four groups of fish, and estrogenization had no effect on gonad weight, ratio of gonad weight to total body weight or egg diameter.

HEMATOCRIT

Despite differences in hematocrit values between control and estrogenized animals, there was no significant difference between control male and female salmon or between estrogenized males and females. From previous work with mammals [11], with birds [9, 19] and with the killifish (*Fundulus heteroclitus*) [22], maturing male salmon would be expected to have higher hematocrit values than maturing females. However, Lysaia [16] has reported that maturing male pink salmon captured in an estuary had a lower red cell count than females in one particular year but a higher count than females in the following year.

Estrogenization resulted in a highly significant decrease in the hematocrit values of both male and female salmon. Since excessive estrogens may cause a positive electrolyte and water balance in mammals [11] the decreased hematocrit values reported here for salmon may be due to hemodilution. Conflicting results have been reported on the effects of estrogens in birds. Thus Domm and Taber [9] demonstrated that large doses of estrogen resulted in a diminution in red blood cell count of castrate female chickens, whereas Sturkie [25] states that estrogen has no effect on the hematocrit of chickens.

CALCIUM AND PROTEIN PHOSPHORUS

It has been demonstrated repeatedly that in all classes of egg-laying vertebrates the levels of serum calcium and protein phosphorus are increased during egg formation or following estrogenization. McDonald and Riddle [17] working with pigeons, and Bailey [1] working with goldfish, have found a correlation between the increased levels of certain calcium fractions and protein phosphorus. Schjeide and Urist [20] have reported that practically all of the serum calcium in estrogenized roosters may be complexed with phosphoprotein, lipoprotein and albumin. However, it has been shown [27] that liver synthesis is the only source of serum phosphoprotein in estrogenized cockerels, and that in functionally hepatectomized estrogenized cockerels there was no correlation between the levels of plasma calcium and protein phosphorus. The present experiment shows that, as in other oviparous vertebrates with intact livers, maturing female salmon have higher serum calcium and protein phosphorus levels than males, and that the levels of both these constituents are increased by exogenous estrogen.

TOTAL PROTEIN AND LIPID CONSTITUENTS

There was no significant difference in the serum levels of total protein, total lipid, neutral lipid, total cholesterol, free cholesterol, esterified cholesterol and lipid phosphorus between control male and female salmon. However, estrogen

increased the levels of all these constituents with the exception of esterified cholesterol. The lack of increased levels in the control females which were under the influence of endogenous estrogen may be attributed to the fact that these are yolk constituents and were probably being utilized by the developing ova at the same rate that they were being produced from body stores. These constituents can not be utilized by the male in the same manner and therefore accumulate in the blood following estrogenization. A similar accumulation in the female following estrogenization may be due to an excess production of these constituents or may in part be a reflection of decreased ovum growth since it has been found [6] that estrogen causes some regression or inhibition of growth of the quiescent ovary of prepuberal pullets.

ACKNOWLEDGMENTS

The authors wish to thank Mr C. T. Shoop and Mr D. Pozar for capturing the fish used in this study and Dr J. R. Brett for helpful advice and criticism of the manuscript.

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Fatty Alcohols from Marine Oils and Segregated Esters¹

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ABSTRACT

Fatty alcohols were prepared by lithium aluminium hydride reduction of the three main methyl ester fractions obtained by countercurrent extraction of methyl esters from herring oil.

Alcohols were also prepared by the same method from commercially important Canadian marine oils, e.g. cod oil, cod liver oil, seal oil, herring oil and dogfish liver oil, and their properties tabulated.

A comparison was made between the sodium reduction method and the lithium aluminium hydride method in the reduction of methyl esters from herring oil and their effect on producing conjugation of the ethylenic double bonds.

INTRODUCTION

IN EARLIER REPORTS from this laboratory (Vandenheuvel and Jangaard, 1957; Jangaard and Vandenheuvel, 1961a) a procedure for continuously producing from marine oils fatty acid methyl esters having specific properties was described. The following components comprise the three fractions obtained from herring oil: fraction I, methyl esters of $C_{14} - C_{16}$ acids; fraction II, esters of $C_{18} - C_{20} - C_{22}$ mono-unsaturated acids; fraction III, esters of $C_{18} - C_{20} - C_{22}$ highly unsaturated acids.

Since any of these varied types of fatty acids may be found randomly arranged in a glyceride molecule in the original oil, no sharp segregation can be obtained using the whole oil. By varying the extraction temperature, flow, and ratio of methyl esters to solvent (nitromethane) the iodine value and composition of the three fractions produced from the corresponding methyl esters can be changed to meet specifications. It was thought that these fractions when converted to alcohols would be of more general interest than alcohols prepared from the whole oil, especially the unique highly unsaturated fraction.

Several workers have reported reducing marine oils to alcohols using the sodium reduction method. Hansley (1947) prepared alcohols from menhaden oil and cod liver oil and Pryde (1951) reported that the recovered menhaden oil alcohols contained 15 to 20% alcohols with conjugated double bonds. Hill *et al.* (1954) lists the alcohols prepared from sardine and menhaden oil and Gruger (1957a) used menhaden and pilchard oil as starting material. Gruger tried fractional distillation, urea inclusion products, and crystallization to fractionate the products.

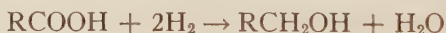
¹Received for publication June 6, 1961.

To our knowledge, no publications have described the properties of alcohols prepared from marine oils using the lithium aluminium hydride method, although Gruger (1957b) pointed out the advantages of this method.

The increased interest in fatty alcohols can be appreciated from the fact that the production in the United States quadrupled in the four years from 1954 to 1958 (Manufacturing Chemists' Assoc., Inc., 1960). This reflects the growth of synthetic detergents in that period, since these represent the largest market for fatty alcohols. Of the earlier detergents, the ones based on lauryl alcohol prepared from cocoanut oil were most common. However, with new processes and raw materials available, a wide variety of fats is used for alcohol production and detergents with superior properties for many specialty uses may be compounded from them (Hill *et al.*, 1954).

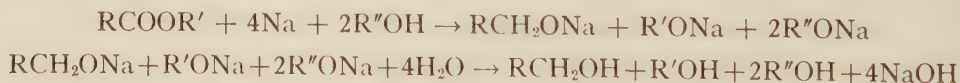
The two principal processes currently in use industrially are the sodium reduction method and hydrogenolysis. In addition a laboratory method utilizing lithium aluminium hydride is available. In all these processes it is economically advantageous to first convert glycerides to simpler (e.g. methyl) esters of the fatty acids because of the ease of recovery of high-purity glycerol in good yield from the simple alcoholysis reaction (Jangaard and Vandenheuvcl, 1961b). In hydrogenolysis the glycerol would be reduced to propylene glycol and 2-propanol if triglycerides were used as raw material and in the sodium reduction process glycerol would have to be recovered from a caustic solution.

In hydrogenolysis, fatty acids, anhydrides, esters or salts are converted to fatty alcohols by contact with hydrogen at high temperatures (200 to 350°C) and pressures (100 to 200 atmospheres) in the presence of a catalyst according to the following equation:



Under these conditions and with the catalysts commonly used (e.g. copper chromite) the double bonds are hydrogenated to give saturated alcohols. More recently it had been claimed that by using larger amounts of catalyst and by adding cadmium salts, the double bonds may be partially or wholly protected and unsaturated alcohols produced (Martinez Moreno *et al.*, 1959). Numerous patents on the process have been granted in the last two decades.

The sodium reduction method makes possible the convenient production of unsaturated as well as saturated alcohols. The procedure is basically the method of Bouveault and Blanc (1903) as modified by Hansley (1947). The overall reaction can be summarized as follows:



The reaction is carried out at atmospheric pressure and consists of adding a solution of dry and neutral ester, reducing alcohol (e.g. methyl isobutyl carbinol) and solvent, usually xylene, to a stirred dispersion of sodium in xylene. The reaction is rapid and exothermic and is controlled by condensing the refluxing

xylene. The unreacted sodium is destroyed with steam, which also decomposes the complex and liberates the alcohols.

Recovery of reducing alcohol and solvent is simplified if the esters are derived from the reducing alcohol, for example fatty acid methyl isobutyl carbinol esters which can be prepared by alcoholysis from the triglycerides (Hill *et al.*, 1954).

A laboratory method for reduction of acids and esters, first described by Nystrom and Brown (1947), employs lithium aluminium hydride (LiAlH_4) in ether solution at room temperature. The excess LiAlH_4 is decomposed with dilute acid and the alcohols are recovered from the ether solution. No appreciable conjugation of the double bonds occurs at these low temperatures and this method is therefore the only one available to produce alcohols from marine oils with the carbon-to-carbon unsaturation unchanged. The reaction can be summarized as follows:



EXPERIMENTAL

SODIUM REDUCTION

Sodium (15.4 g) and freshly dried xylene (53 ml) were placed in a 1-litre 3-necked flask equipped with a stirrer driven by a powerful air motor. The flask was fitted with a dropping funnel and reflux condenser with drying tube and heated by an electric mantle. The sodium was melted and finely dispersed with rapid stirring. Methyl esters (50 g) and methyl isobutyl carbinol (42 ml) in xylene (150 ml) were added from a dropping funnel, the heat of reaction being removed by refluxing. By using these large amounts of solvent the reaction was easily controlled and the danger of gelling was diminished. The addition was completed in 15 to 20 min and the refluxing and stirring were continued for another 40 min.

The reaction mixture was then hydrolyzed by introducing small amounts from a dropping funnel into a hydrolysis flask where the mixture was kept boiling the admission of steam. The excess sodium decomposed smoothly, and the xylene + methyl isobutyl carbinol was removed by the steam distillation. The organic layer separating in the flask was washed with brine, and the alcohols were distilled under vacuum. The soaps remained in the residue.

Difficulties with gelling due to soap formation will be encountered if (1) the starting material contains an appreciable amount of free fatty acids, and (2) the solvents, esters, and apparatus have not been thoroughly dried and protected against moisture.

In a case when the reaction mixture had gelled and could not be dropped into the hydrolysis flask, the excess sodium was decomposed with anhydrous methanol (500 ml, somewhat more than necessary to dissolve the gel). Water (300 ml) was added to decompose the complex and the mixture was shaken in a separatory funnel. Petroleum ether (250 ml) was then added, and the fatty alcohol + petroleum ether + xylene + methyl isobutyl carbinol layer was washed with water. The solvents were then removed under vacuum and the

alcohols vacuum-distilled. By using this procedure the amount of conjugation of the double bonds was found to be considerably reduced.

The yields in both cases were about 85% of the theoretical.

LITHIUM ALUMINIUM HYDRIDE REDUCTION

Reagent ethyl ether was dried by distillation over LiAlH_4 , then 30 g LiAlH_4 was added to 1000 ml of the distillate and refluxed for 6 hours. The solution was stored in 100-ml bottles with polyethylene-lined caps.

One hundred millilitres of the solution containing approximately 3 g LiAlH_4 was added to dried ether (50 ml) in a 1000-ml 4-necked flask under a stream of nitrogen. The flask was equipped with a stirrer, a reflux condenser and a dropping funnel.

Thirty grams of oil or methyl esters was dissolved in 100 ml anhydrous ether and added from the dropping funnel with rapid stirring over a period of approximately 20 min and the reaction mixture was refluxed for another 30 min. After cooling it in an ice bath, 30 ml of 10% H_2SO_4 and 50 ml water were added slowly to decompose the excess LiAlH_4 . Efficient stirring is essential at this point to break any gel that may form. The acidified mixture was transferred to a separatory funnel and the water layer extracted with ether. The ether layer was washed with water until neutral to litmus, dried over sodium sulphate and the ether evaporated. The alcohols were then vacuum-distilled. The yields were of the order of 95 to 99% of the theoretical.

The saponification value, iodine value, free fatty acids and unsaponifiable matter of all products were determined according to the American Oil Chemists' Society Official Methods (1946).

The hydroxyl values were determined using Verbeck's pyridine-phthalic anhydride method (1947). The ultraviolet absorption spectra for conjugated constituents were determined in *iso*-octane with a Beckman DK-2 spectrophotometer.

The gas chromatographic analyses of the acetylated alcohols (Link *et al.*, 1959) were performed on a Wilkins Aerograph, column packing DEGS polyester substrate, 25% on Chromosorb, column dimensions $\frac{1}{4}$ inch by 10 feet (6 mm by 3 m), oven temperature 210°C.

RESULTS AND DISCUSSION

Table I lists the physical constants of methyl esters from whole herring oil and of the three ester fractions obtained by countercurrent segregation using

TABLE I. Physical constants of methyl esters.

	Iodine value	Refractive index at 25°C	Saponi- fication value	Free fatty acids	Unsaponi- fiable matter	Av. mol. wt. of fatty acids from sap. value
Methyl esters from herring oil	134.5	1.45645	189.0	0.05	0.9	284
Segregated methyl esters:						
Fraction I	39.8	1.44250	208.7	0.6	<0.1	256
Fraction II	117.9	1.45670	180.6	0.3	<0.1	297
Fraction III	233.8	1.46930	185.7	0.7	<0.1	290

nitromethane; Table II gives the constants for the fatty alcohols produced by LiAlH_4 reduction of these esters.

TABLE II. Physical constants of alcohols reduced from methyl esters using lithium aluminium hydride.

Alcohols from	Iodine value	Refractive index at 25°C	Distilling range at 0.2 mm	Hydroxyl value	Hydroxyl (OH) %	Free fatty acids %	Saponification value	Av. mol. wt. from OH value
			°C					
Methyl esters from herring oil	146.0	1.46443	120–170	207.6	6.29	0.04	0.6	270
Segregated methyl esters:								
Fraction I	43.9	(solid)	118–138	229.7	6.96	0.06	0.6	244
Fraction II	132.7	1.46500	136–170	198.1	6.00	0.09	0.8	283
Fraction III	255.9	1.47810	130–174	199.7	6.05	0.08	1.0	280

Figure 1 gives the gas chromatographic analysis of acetylated alcohols prepared from three fractions with tentative identification of some of the major component peaks.

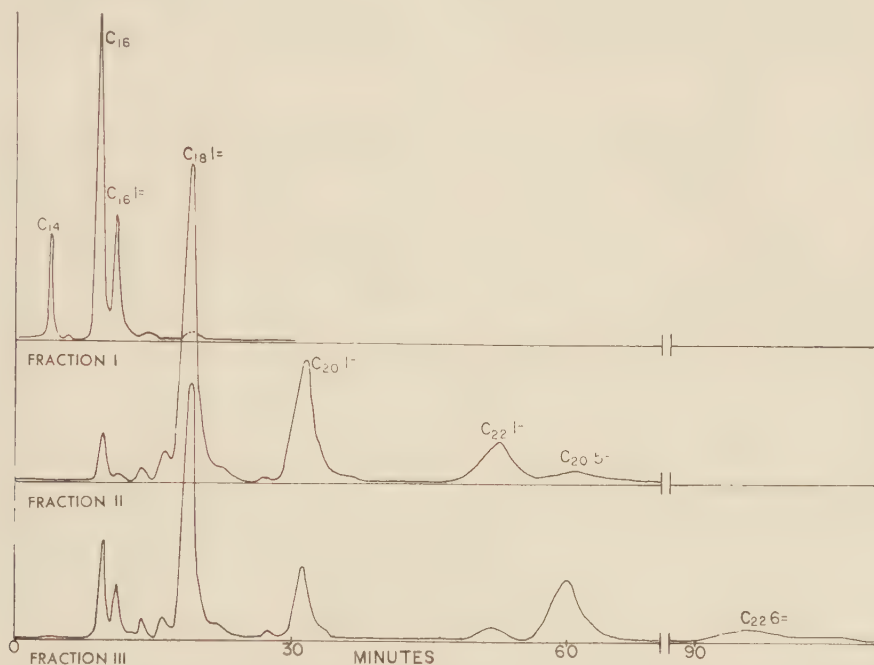


FIG. 1. Gas chromatograms of acetylated alcohols from methyl ester fractions from herring oil, with tentative identification of some of the peaks. Sample size I: 0.001 ml; II and III: 0.004 ml.

Fraction I alcohol is a white solid at room temperature and contains mainly C_{14} – C_{16} saturated alcohols with smaller amounts of C_{14} – C_{16} – C_{18} alcohols with one double bond.

Fraction II is a colourless, oily liquid with a slight odour. It contains a high percentage of the mono-unsaturated alcohols of the C_{18} – C_{20} – C_{22} series, but also

a small amount of those of higher unsaturation. A slight selective hydrogenation to an iodine value of 90 to 100 from the original 133 should give a fraction containing 70 to 80% mono-unsaturated $C_{18} - C_{20} - C_{22}$, the remainder being saturated and diene alcohols.

Fractions I and II are similar to alcohols obtained from vegetable and animal fats, and are used in the production of detergents, cosmetics, lubricant additives, defoamers and chemical intermediates. However, fraction III is unique and contains most of the highly unsaturated alcohols with 3, 4, 5 and 6 double bonds typical of the marine oils. It is a pale yellow oily liquid with a "fishy" odour. Because of its high unsaturation, it should be of interest as a chemical intermediate in protective coatings, organic synthesis and surfactant manufacture and also in pharmaceutical applications.

In Table III the physical constants of some commercially important marine oils of Canadian origin are given and in Table IV the constants of the alcohols prepared from them by $LiAlH_4$ reduction. All these alcohols are colourless to straw-coloured, slightly viscous liquids with slight "fishy" odours. However, in most cases the odours are much milder and less offensive in the alcohols than in the starting material.

TABLE III. Physical constants of marine oils used for reduction.

Type of oil	Iodine value	Refractive index at 25°C	Saponification value	Free fatty acids	Unsaponifiable matter
				%	%
Cod oil, sunrotted, Newfoundland	168.9	1.47678	187.5	10.5	1.3
Cod liver oil, Newfoundland	170.3	1.47780	185.4	0.8	1.5
Cod liver oil, solvent-extracted in laboratory	182.7	1.47919	182.7	0.5	1.2
Herring oil, British Columbia	136.9	1.47360	189.6	1.1	1.0
Seal oil, harp seal	149.7	1.47478	192.0	0.7	0.3
Dogfish liver oil, British Columbia	117.2	1.47165	161.3	1.2	15.6

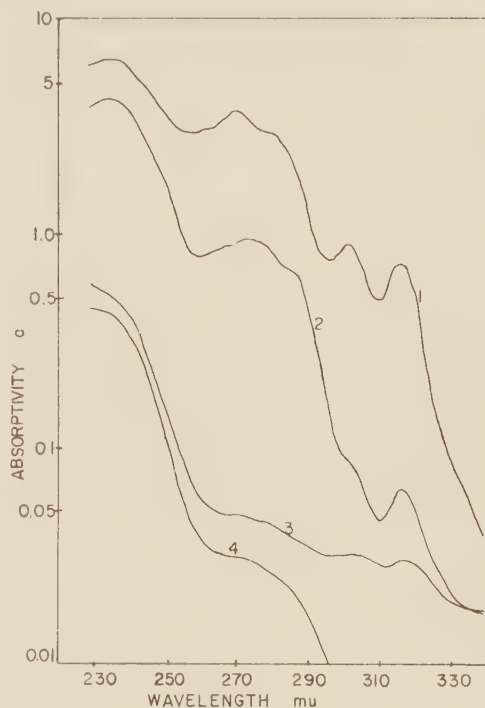
TABLE IV. Physical constants of fatty alcohols, lithium aluminium hydride reduction.

Alcohols from	Iodine value	Refractive index at 25°C	Distilling range at 0.2 mm °C	Hydroxyl value	Hydroxyl (OH) %	Saponification value	Free fatty acids	Av. mol. wt. from OH value
							%	%
Cod oil, sunrotted, Nfld.	180.5	1.46852	116-165	196.4	5.95	0.37	0.11	286
Cod liver oil, Nfld.	182.0	1.46866	116-162	198.1	6.00	0.73	0.06	283
Cod liver oil, solvent-extracted in laboratory	197.5	1.47040	120-167	199.4	6.04	0.73	0.09	282
Herring oil, B.C.	146.5	1.46458	120-175	204.6	6.20	0.09	0.10	274
Seal oil, harp seal	161.9	1.46620	122-167	204.9	6.21	2.09	0.16	274
Dogfish liver oil, B.C.	124.0	1.46357	120-174	211.9	6.42	0.63	0.11	265

To compare the two commonly used laboratory methods, sodium and $LiAlH_4$ reductions, a few sodium reductions were performed on the methyl esters from herring oil. In one of the experiments the reaction mass was added to boiling water and the solvents were steam distilled as recommended by Hansley. In a second experiment, the excess sodium was decomposed with anhydrous methanol as described above. Much less conjugation of the double bonds was found in the

FIG. 2. Conjugation of double bonds in alcohols reduced from methyl esters from herring oil.

1. Sodium reduction, excess sodium decomposed with steam.
2. Sodium reduction, excess sodium decomposed with methanol.
3. Methyl esters.
4. Lithium aluminium hydride reduction.



alcohols prepared by the latter method, indicating that most of the conjugation takes place in the steam hydrolysis and distillation step, as well as in the reduction proper. Figure 2 shows the ultraviolet absorption curves of these samples (in *iso*-octane), of the alcohols prepared by the LiAlH_4 method, and also of the original methyl esters. In the LiAlH_4 method there is actually a slight lessening in the amount of conjugation, due probably to the reduction of peroxides and other materials.

An attempt was made to calculate the actual percentage of conjugated constituents using the formulas given in A.O.C.S. Official Methods for glycerides, esters, and fatty acids. No formulas are given for fatty alcohols, so the values can only be approximate. The results are summarized in Table V.

TABLE V. Total conjugated constituents in methyl esters and alcohols.

Type of bond	Original methyl esters from herring oil		Alcohols					
			Sodium-reduced steam distilled		Sodium-reduced methanol added		LiAlH ₄ -reduced	
	A*	C*	A	C	A	C	A	C
		%		%		%		%
Conjugated diene	0.5	0.45	6.5	5.9	4.3	3.9	0.4	0.36
Conjugated triene	...	...	1.76	0.083	0.28	0.13	...	...
Conjugated tetraene	...	...	0.85	0.38	0.02	0.01	...	...
Conjugated pentaene	...	...	...	trace	...	...	...	...
Total conjugated material	—	0.45	—	7.11	—	4.04	—	0.36

*A = absorptivity; C = conjugated alcohols.

The data in Table V show that a decrease of conjugation to almost one-half can be achieved by eliminating or shortening the steam treatment of the reaction mass. Even so, the total conjugation with the sodium reduction method is more than ten times as high as in the alcohols prepared by LiAlH_4 reduction.

SUMMARY

The properties of fatty alcohols from fatty-acid methyl ester fractions from herring oil and several commercially important marine oils are tabulated.

Some decrease in the conjugation using the sodium reduction method could be effected by decomposing the excess sodium with methanol and vacuum-distilling the solvents, as compared to the water quenching and steam distillation procedure in use commercially.

The lithium aluminium hydride reduction method is the only procedure whereby fatty alcohols can be prepared from marine oils without some changes in the ethylenic double bonds taking place.

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Growth and Age Determination of the Pacific Edible Crab *Cancer magister* Dana¹

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ABSTRACT

Of 2,820 early post-larval unsexed crabs collected by small-meshed trawl in two regions of the Queen Charlotte Islands, 1,175 were measured and the 1st and 2nd post-larval instars were identified as modes at 6.9 and 10.0 mm, respectively. Increments of 5 unsexed moulted crabs, carapace widths 6.80 to 9.96 mm, were from 36.3 to 46.5%. A total of 284 males, from 83 to 186 mm, moulted in crab traps, live-wells, and while at large as tagged specimens; 44 females, from 88 to 145 mm, moulted in traps. Using equations of regression of new carapace width on old width for both sexes and starting at the 2nd instar, average carapace widths were calculated for instars 3 to 15. In the width-frequency distributions of 8,145 crabs, separation of stages was sufficient for identification of age-groups. It is estimated that a year after hatching, males reach stage 5 or 6 (24.2 or 31.1 mm); after 2 years stage 11 or 12 (96.6 or 119.5 mm) is attained; after 3 years stage 13 (146.9 mm); after 4 years most males are in the 14th stage (176.2 mm) and above the British Columbia legal size of 165 mm; and generally after 5 years males are in stage 15 (207.5 mm). Growth of females is similar for 2 years, but afterwards is slower.

INTRODUCTION

THE FIRST STUDY of the growth of the Pacific edible crab, *Cancer magister*, was conducted by MacKay and Weymouth (1935). On the basis of measurements and moulting records of crabs from Boundary Bay in southern British Columbia, they were able to determine growth rate and estimate age. Male crabs were found to pass through 17 post-larval instars, attaining maturity at 4 or 5 years, and reaching the British Columbia legal size, 6½ inches or 165 mm in carapace width, after 7 or 8 years. Sixteen instars were required for maturity of females, which mature at about the same age as males but rarely reach legal size.

Cleaver (1949), using moulting records and measurements from the coast of Washington, found a more rapid growth than MacKay and Weymouth. Most individuals of both sexes attained maturity after 3 years; and males had reached legal size (169 mm in Washington) in the 14th or 15th instar, after 4 years. Growth of females for the first 2 years was similar but subsequently the rate was uncertain.

From 1949 to 1957, as part of a crab investigation in the Queen Charlotte Islands, British Columbia, the writer has attempted to determine growth and age.

SAMPLING OF EARLY POST-LARVAL CRABS

The reproductive cycle of the edible crab in the Queen Charlotte Islands has been described (Butler, 1956). Breeding occurs during the summer; fertilized ova are extruded by the female in early autumn and are carried until hatching in the spring, about April. The larval life lasts about 4 months. The megalops

¹Received for publication September 21, 1960.

is found during August, and metamorphosis into the first post-larval stage occurs during September.

From 1953 to 1956 early post-larval crabs were collected in Naden Harbour and McIntyre Bay, off the north coast of Graham Island. Most sampling was carried out with a small trawl having a beam 80 inches (2.03m) long and constructed of cotton netting of $\frac{1}{2}$ -inch stretched mesh. Tows were made during daylight hours and lasted 10 minutes. Crabs were taken most abundantly on sand bottom in inshore regions shallower than 10 fathoms (18 m) (Fig. 1); 2,820 post-larval crabs were taken in 143 tows.

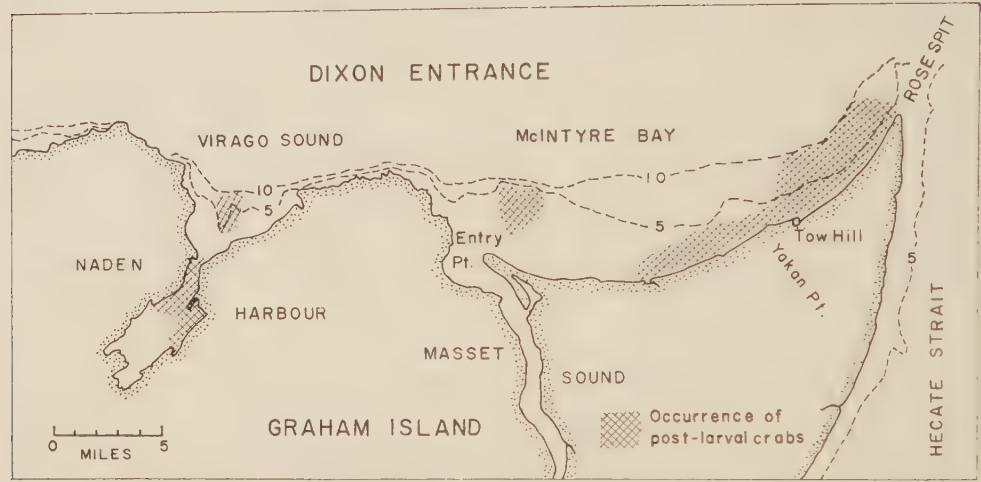


FIG. 1. Map showing the distribution of early post-larval crabs in Naden Harbour and McIntyre Bay, 1953 to 1956. Depths in fathoms.

MOULTING OF POST-LARVAL CRABS. Of about a dozen post-larval crabs which were placed in bottles of sea water immediately after capture, 5 moulted successfully. Four individuals passed from the 1st into the 2nd post-larval stage, and the other from the 2nd into the 3rd stage. Measurements of the carapace width, including the 10th antero-lateral spines, were made with vernier calipers which were accurate to 0.02 mm (Table I). No attempt was made to determine sex of these early stages.

TABLE I. Increase in size of post-larval crabs at moulting.

Instar	Carapace width		Increase	
	Old	New		
	mm	mm	mm	%
1	6.80	9.96	3.16	46.5
1	6.56	9.44	2.88	43.9
1	6.76	9.86	3.10	45.9
1	6.40	8.72	2.32	36.3
Av.	6.63	9.50	2.87	43.2
2	9.96	14.04	4.08	41.0

MEASUREMENT OF EARLY POST-LARVAL STAGES. A sample of 1,175 post-larval crabs, collected in McIntyre Bay from August 29 to September 9, 1953, were measured with vernier calipers. Measurements were rounded to the nearest 0.1 mm, and are plotted in Fig. 2.

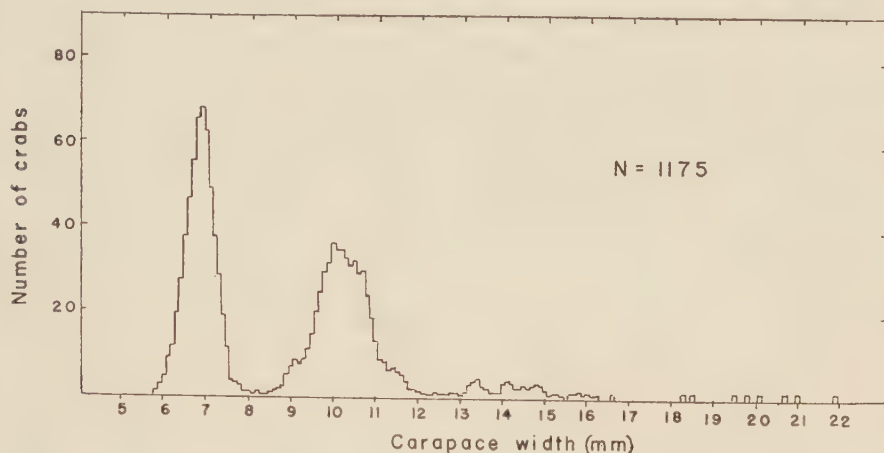


FIG. 2. Carapace width frequency distribution of unsexed post-larval crabs collected in McIntyre Bay, September, 1953.

First post-larval stage crabs range from 5.8 to 8.0 mm, with the mode at 6.9 mm. Carapace widths of the 2nd stage are from 8.2 to about 12.5 mm, and the mode appears at 10.0 mm. Individuals between 13 and 16 mm presumably belong to the 3rd stage, and the remainder in the distribution between 18 and 22 mm are likely 4th stage crabs.

GROWTH PER MOULT OF LARGER CRABS

Moulting records were obtained from several sources. Crabs moult in crab traps and since it is possible to match soft-shelled individuals with their cast-off exoskeletons, increments were determined. Specimens were taken from traps and placed in live-wells where ecdysis occurred within a day or two. Male crabs were marked with a type of tag retained through moulting (Butler, 1957). Some recovered individuals moulted once during their periods of freedom, enabling increments to be determined. A total of 284 male and 44 female records was obtained, as follows:

	<i>Males</i>	<i>Females</i>
Moulted in traps	250	44
Moulted in live-wells	22	...
Tag recoveries	12	...

All crabs moulting in traps and live-wells were caught on fishing grounds in Hecate Strait and McIntyre Bay between 1953 and 1957. Of 12 moulted tagged crabs recovered in 1956, 1957, and 1959, 11 were taken in the above two areas, and the other in Naden Harbour. Male moulting records were all considered together, as there were no apparent differences according to locality.

Carapace widths before moulting of all but one male were from 83 to 186 mm; the other was 29 mm. Records were grouped by 5-mm intervals and are summarized in Table II. Absolute and percentage increments are graphed in Fig. 3. Moulting records of females, from 88 to 145 mm, are summarized in Table III. Over this size range, the increments decrease from 24 to 16 mm, or from 27.3% to 11%. Thus, absolute increase per moult of males larger than 90 mm increases with size, whereas successive increments of the females decrease.

TABLE II. Average carapace widths, absolute increments, and percentage increments, for male crabs; also the range of new-shell widths, and of increments.

Size	Crabs	Carapace width		Increment		Ranges	
		Old	New			Width	Increment
<i>mm</i>	<i>No.</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>	%	<i>mm</i>	<i>mm</i>
	1	29.0	37.0	8.0	27.6	...	...
80-84	1	83.0	107.0	24.0	28.9	...	...
85-89	3	88.7	113.0	24.3	27.4	110-115	21-26
90-94	2	92.0	117.0	25.0	27.2	115-119	23-27
95-99	6	97.5	123.5	26.0	26.7	121-125	24-28
100-104	2	101.5	124.5	23.0	22.7	124-125	21-25
105-109	3	106.0	133.7	27.7	26.1	131-135	26-30
110-114	3	111.0	137.3	26.3	23.7	133-141	22-29
115-119	3	116.3	144.0	27.7	23.8	140-149	25-30
120-124	2	122.0	149.0	27.0	22.1	144-154	24-30
125-129	7	128.3	156.7	28.4	22.1	153-159	24-31
130-134	15	131.7	160.2	28.5	21.6	154-165	23-31
135-139	11	136.6	165.7	29.1	21.3	162-172	27-34
140-144	22	142.1	172.4	30.3	21.3	164-179	23-35
145-149	32	146.5	177.4	30.9	21.1	171-182	25-35
150-154	43	151.9	182.2	30.3	19.9	168-189	17-36
155-159	53	157.0	186.5	29.5	18.8	174-192	16-35
160-164	44	162.1	191.5	29.4	18.1	170-199	10-35
165-169	15	167.2	197.2	30.0	17.9	189-206	22-38
170-174	6	172.2	199.3	27.1	15.7	195-203	22-31
175-179	5	176.2	208.8	32.6	18.5	203-213	28-35
180-184	4	181.8	211.5	29.7	16.3	208-216	25-35
185-189	1	186.0	218.0	32.0	17.2	...	...

TABLE III. Average carapace widths, absolute increments, and percentage increments, for female crabs; also the range of new-shell widths, and of increments.

Size	Crabs	Carapace width		Increment		Ranges	
		Old	New			Width	Increment
<i>mm</i>	<i>No.</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>	%	<i>mm</i>	<i>mm</i>
85-89	1	88.0	112.0	24.0	27.3	...	...
90-94	1	93.0	113.0	20.0	21.5	...	...
95-99	1	99.0	123.0	24.0	24.2	...	...
100-104	1	100.0	117.0	17.0	17.0	...	...
115-119	1	117.0	136.0	19.0	16.2	...	...
125-129	12	127.0	145.1	18.1	14.3	136-149	11-22
130-134	11	132.4	149.8	17.4	13.1	146-152	15-20
135-139	10	137.2	153.9	16.7	12.2	148-158	13-21
140-144	5	141.6	158.2	16.6	11.7	155-161	15-19
145-149	1	145.0	161.0	16.0	11.0	...	...

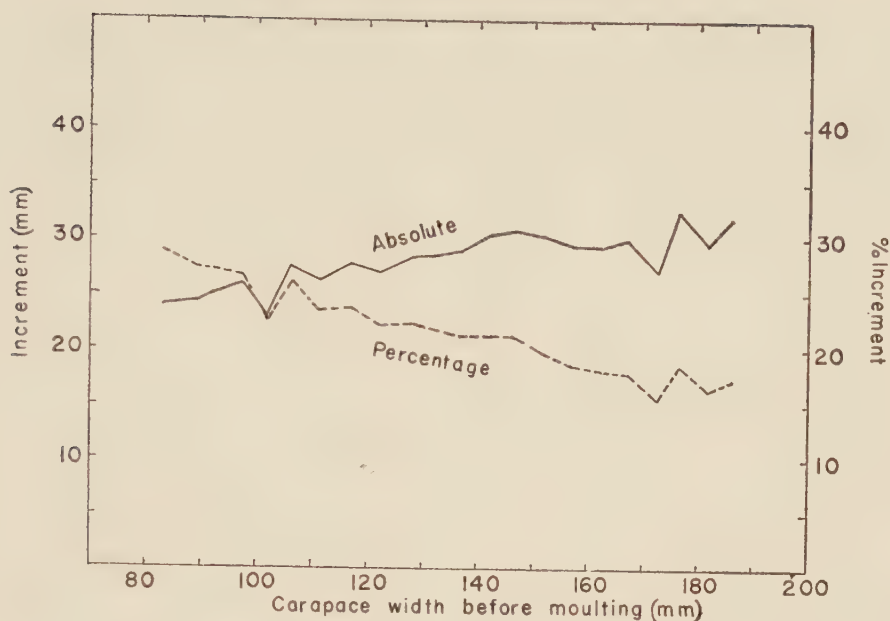


FIG. 3. Absolute and percentage increments at moulting of male crabs.

DETERMINATION OF INSTAR SIZES

For early post-larval stages, and for larger crabs, carapace width before moulting was plotted against carapace width after moulting (Fig. 4). Straight lines were fitted by least squares, of the general form:

$$Y = aX + b \quad (1)$$

Y is carapace width in millimetres after moulting, and X is the same before moulting; a and b are fitted constants.

For unsexed and male (6.63–29 mm):

$$Y = 1.22X + 1.62 \quad (3)$$

For males (83–186 mm):

$$Y = 1.07X + 19.00 \quad (3)$$

For females (88–145 mm):

$$Y = 0.892X + 31.58 \quad (4)$$

Lines (3) and (4) intersect (2). The points of intersection represent inflexions or abrupt changes in growth rate. They may be taken from Fig. 4, or calculated by the method of Kurata (1960), as follows. Let the constants of line (2) above be a and b , and those for (3) or (4) be a' and b' ; then the point of intersection of the two lines, L , is:

$$L = \frac{b' - b}{a - a'} \quad (5)$$

The intersects, 115.9 mm for males and 90.8 mm for females, agree reasonably well with sizes at maturity determined earlier (Butler, 1960), hence it is likely that the change in growth rate is associated with sexual maturity. The long extrapolation of line (2) seems justified because it conforms with the general pattern of growth in Crustacea generally (Kurata, op cit.) and for *C. magister* specifically, as shown later.

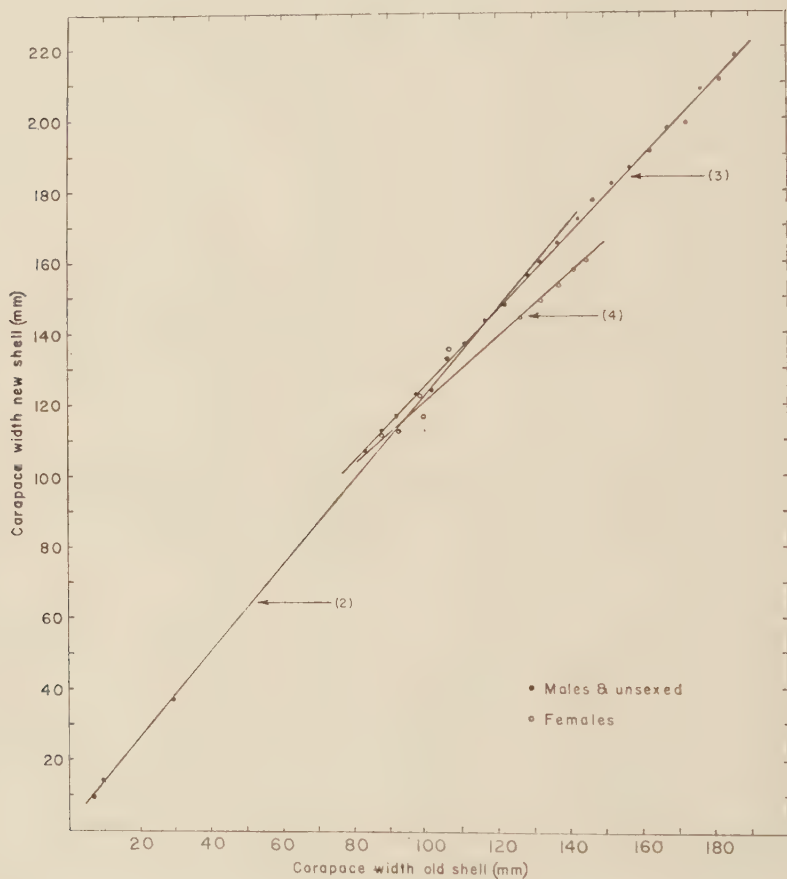


FIG. 4. Increases in carapace width as expressed by equations 2-4 of the text.

Starting with the 2nd post-larval stage at a carapace width of 10 mm, equation (2) was used to calculate instar sizes up to the 12th instar for males; and instars 13 to 16 were determined by equation (3). Likewise, female instar sizes up to the 11th were calculated from equation (2), and the rest up to 16 from (4). Calculated carapace widths are given in Table IV.

TABLE IV. Comparison of instar sizes of *Cancer magister*. Measurements are of carapace widths, including 10th spines.

Instar	Washington (Cleaver)		Southern B.C. (MacKay and Weymouth)		Queen Charlotte Islands	
	♂	♀	♂	♀	♂	♀
No.	mm	mm	mm	mm	mm	mm
1	(5-7)	(5-7)	5.2	5.2	6.9	6.9
2	9.4	9.4	7.4	7.4	10.0	10.0
3	12.5	12.5	9.7	9.7	13.8	13.8
4	16.8	16.8	13.4	13.4	18.5	18.5
5	23.5	23.5	18.2	18.2	24.2	24.2
6	30.4	30.4	24.0	24.0	31.1	31.1
7	37.2	37.2	31.5	31.5	39.6	39.6
8	47.2	47.2	41.0	41.0	49.9	49.9
9	59.8	59.8	52.5	52.5	62.5	62.5
10	72.8	72.8	65.7	65.7	77.9	77.9
11	90.6	90.6	80.5	80.5	96.6	96.6
12	113.4	113.4?	95.8	95.8	119.5	117.8
13	138.4	126.0?	112.6	112.6	146.9	136.6
14	165.9	137.0?	130.0	127.3	176.2	152.5
15	(188?)	...	149.6	141.3	207.5	167.6
16	...	...	170.8	153.5	241.0	181.1
17	...	...	190.1	...	...	...

ESTIMATE OF AGE

The number of instars which both sexes may be expected to pass through has been determined, but no data which bear directly on frequency of moulting or time spent in various instars are available. In an attempt to estimate age, the calculated instar sizes have been superimposed on carapace width frequency distributions. A total of 8,145 crabs were used for this study, collected between 1950 and 1956 by traps, trawls and dip-nets along the beach. Crabs were measured with sliding brass calipers, accurate to the nearest millimeter.

At metamorphosis crabs are about 5 months old, calculated from time of hatching in April. It is not known which stage the early post-larval stages reach before the onset of winter, and whether moulting occurs during the colder months. No sample of juvenile stages has been taken between September and June. Size frequency distributions are shown of both male and female crabs collected near Masset during June, 1950. On June 3 (Fig. 5A, 6A) most individuals appeared to be in the 2nd and 3rd stages; on June 28, 3rd-stage crabs were most prevalent with others apparently belonging to 4th and 5th stages (Fig. 5B, 6B). One other sample taken during June 26-27, 1956 (Fig. 5C) included 4 males between 24 and 43 mm which seemed to be in stages 5 to 7. Four samples collected during the month of July in 1951, 1953 and 1954 (Fig. 5D-F, 6C-E) show males and females from 23 to 70 mm in stages 5 to 9. A sample from Naden Harbour taken from August 29 to September 4, 1954, had males from 43 to 75 mm in stages 7 to 10; and females from 40 to 78 mm which apparently fall into stages

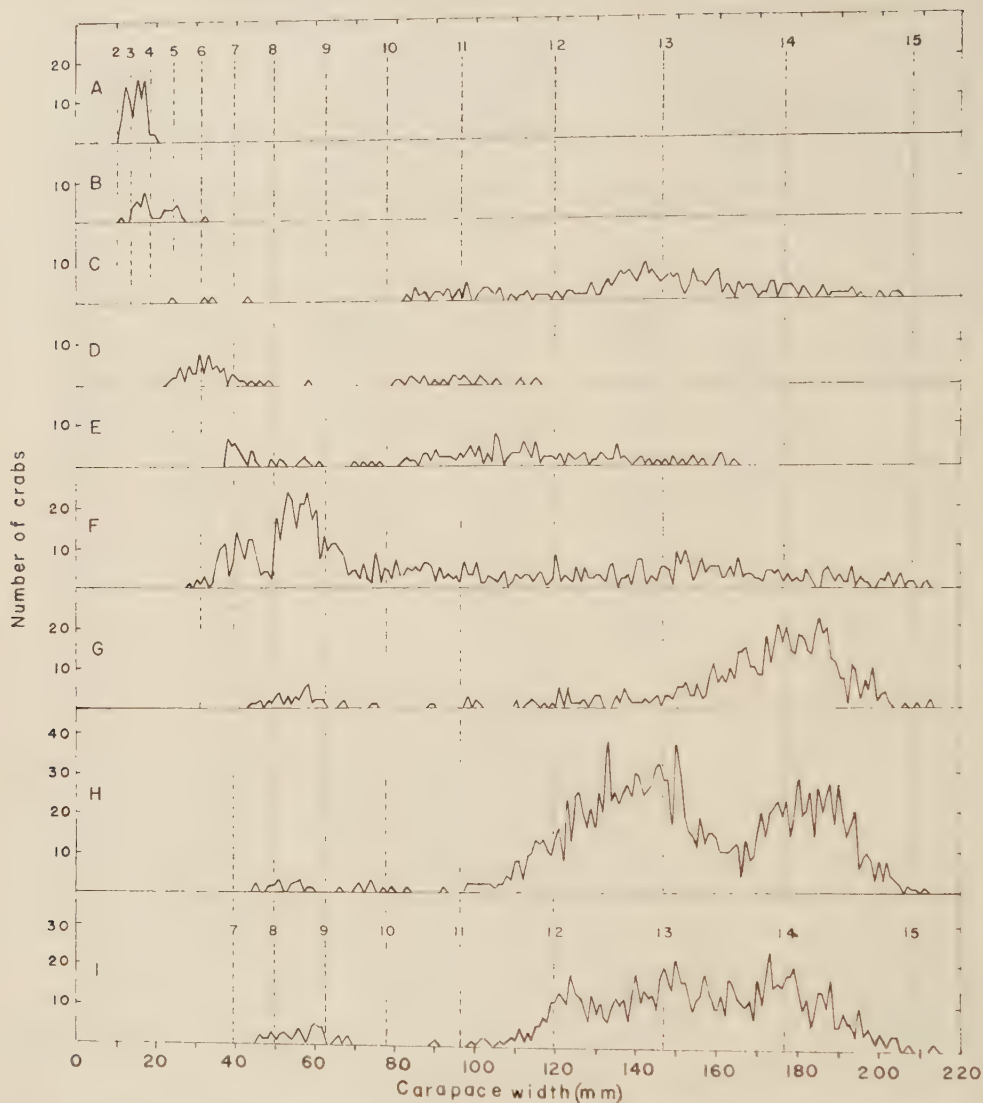


FIG. 5. Carapace width frequency distributions of male crabs collected between June 3, 1950 and September, 1956. Vertical lines represent positions of calculated instars. Sections A and B, Masset, June 3 and 28, 1950; D, Yakan Point, July 12 and 17, 1951; E and F, Hecate Strait, July 9-14, 1954, July 7-20, 1953; C, G, H, I, Naden Harbour, June 26-27, 1956, August 29-September 4, 1954, September 11-23, 1955, September 16-22, 1956.

7 to 10 (Fig. 5G, 6F). In September, 1955, and 1956 (Fig. 5H, I) males from Naden Harbour ranged from 45 to 83 mm which seemed to be in stages 7 to 10 and females (Fig. 6G, H) appeared to fall into stages from 7 to 10.

Thus young crabs which metamorphose in September may range from 15 to 30 mm, stages 3 to 6, by the following June about 8 months later. By the

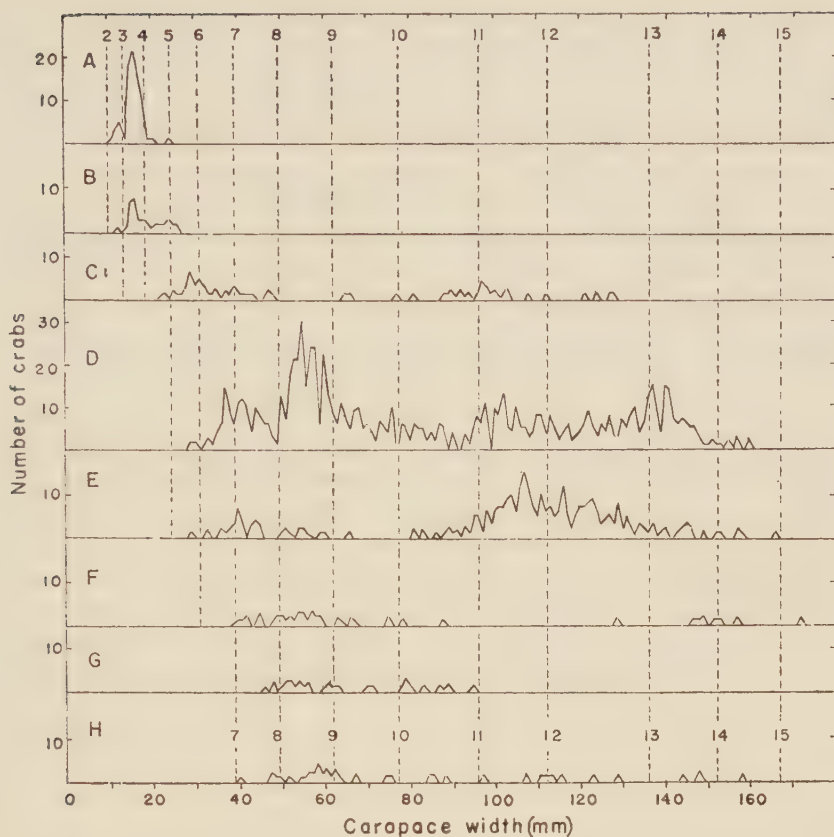


FIG. 6. Carapace width frequency distributions of female crabs collected between June 3, 1950 and September, 1956. Vertical lines represent positions of calculated instars. Sections A and B, Masset, June 3 and 28, 1950; C, Yakan Point, July 12 and 17, 1951; D and E, Hecate Strait, July 7-20, 1953, July 9-14, 1954; F, G, H, Naden Harbour, August 29-September 4, 1954, September 11-23, 1955, September 16-22, 1956.

end of the summer, a year after metamorphosis or about 17 months after hatching the fastest growing individuals in the group may be about 80 mm, and in the 9th or 10th stages.

The combined sample taken on July 12 and 17, 1951, at Yakan Point (McIntyre Bay) and Masset, respectively, shows a group of males between 80 and 115 mm which seemed to fall mostly into stage 11 (Fig. 5D); the majority of females occurred in a group between 80 and 110 mm and probably belonged to stage 11 (Fig. 6C). The frequency distribution of male crabs measured during July, 1954, in Hecate Strait (Fig. 5E) showed a fairly prominent group between 82 and about 115 mm, which seemed mostly to be in stage 11. The picture is less clear for the female distribution in the same sample (Fig. 6E);

individuals of 81 mm and larger were found which may have been in stages 10 to 12. Male crabs from Naden Harbour taken during June, 1956, (Fig. 5C) ranging from 83 to about 130 mm, seem to belong to the 10th and 11th stages. Another sample from the same region about 3 months later (Fig. 5I) shows the lack of males between 80 and 100 mm, in the 10th or 11th stages and the prominence of those between 110 and 130 mm, belonging to stage 12. Also in the sample collected in September, 1955, (Fig. 5H) a paucity of stage 11 males seemed apparent; although there is no clear separation of 110–155 mm males into stages, some grouping of those between 110 and 130 mm is indicated. During August and September, 1954, in Naden Harbour (Fig. 5G) there were relatively few male crabs between 80 and 110 mm, where stage 11 individuals are assumed to be. The same distribution shows a fairly discrete group present between 110 and 130 mm, presumably stage 12. Thus 2 years following metamorphosis, or 29 months after hatching, most male crabs probably have reached stage 12, with fewer in the 11th stage. Fewer measurements are available of females but after 2 years they are probably much the same size as males.

On June 15, 1953, 535 cast-off male exoskeletons from 93 to 175 mm were found at Yakan Point (Fig. 7). There is a prominent group in the distribution between 109 and 138 mm probably belonging mostly to stage 12 with some overlap of 13th stage males. It is likely then that these crabs had reached stage 12 the preceding autumn, passed the winter and spring in this stage and had moulted

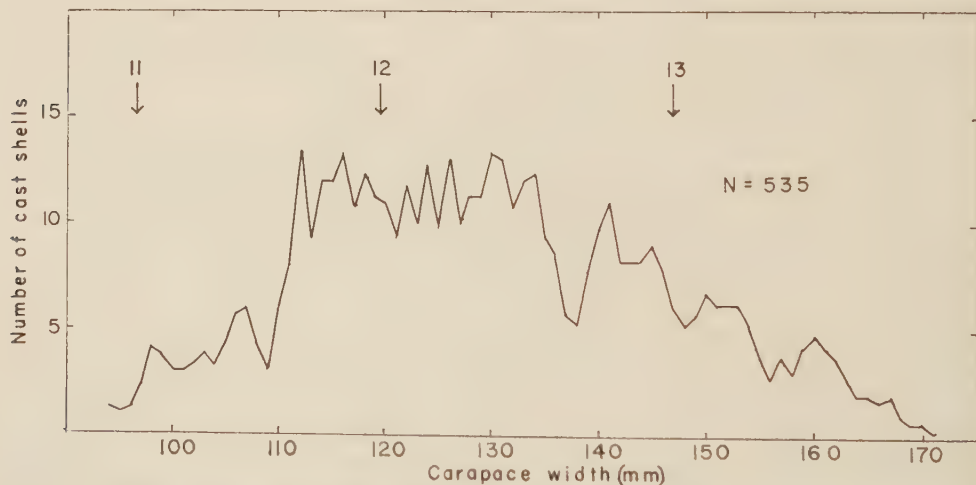


FIG. 7. Cast-off shells of male crabs measured at Yakan Point (McIntyre Bay) June 15, 1953. Positions of calculated instars shown by numbered arrows.

just prior to sampling. A small number of males about to moult and soft-shelled specimens observed at the same time indicate that the sample of cast-off exoskeletons represented current conditions. Figure 8 shows a sample of male crabs caught in McIntyre Bay early in July, 1956, made up entirely of individuals

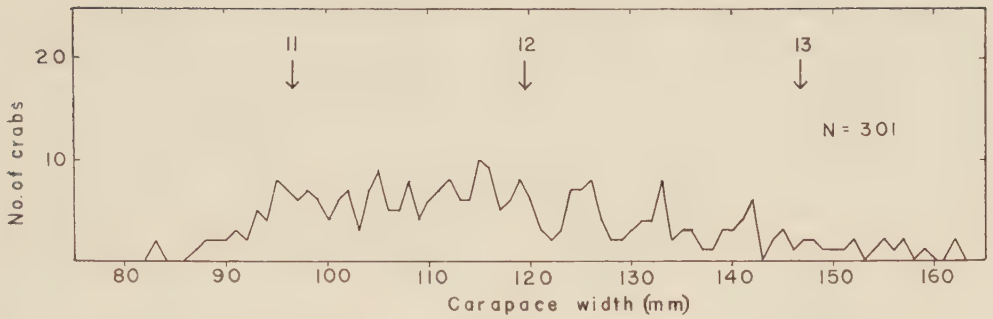


FIG. 8. Carapace width frequency distribution of male crabs, about to moult, McIntyre Bay, July 4-5, 1956. Positions of calculated instars shown by numbered arrows.

about to moult². These males range from 83 to 162 mm but there is an indication of a group between 92 and 122 mm apparently in stages 11 and 12. Thus, both 1953 and 1956 samples are evidence that passage from the 12th to the 13th stage occurs during early summer, and moreover there is no indication that these males, now in their fourth summer, will moult again for another year. Samples from Naden Harbour during September, 1956 and 1955 (Fig. 5G, H), have definite groups, about 130 to 155 mm, which seemed to consist of stage 13 males, attained 3 years after metamorphosis or about 41 months after hatching.

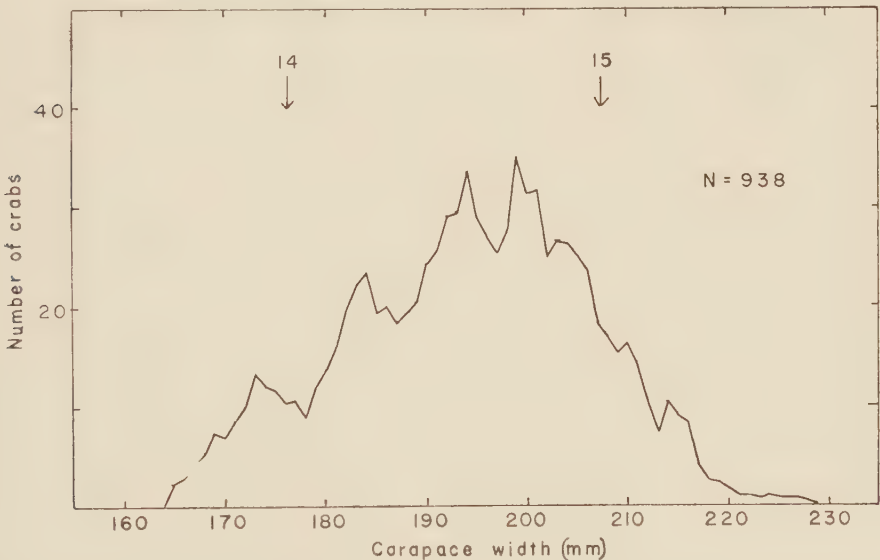


FIG. 9. Carapace width frequency distribution of male crabs sampled from commercial catch, McIntyre Bay, May 16, 1956. Positions of calculated instars shown by numbered arrows.

²In these males the carapace had separated along the pleural groove or epimeral line on the antero-lateral and postero-lateral margins; and there was splitting along the absorption lines on the large segments of the chelipeds.

Maturity of females is reached at a carapace width of about 100 mm (Butler, 1960) in the 11th or 12th stages at the end of 2 years; after then, it is not certain whether females moult annually. Measurements of larger females are mostly lacking but that ecdysis is less frequent is indicated by observations of fouling on exoskeletons, which at times is heavy.

If it be postulated that males remain in the 13th stage for about a year, then stage 14 is reached during the 5th summer between 4 and 4½ years after hatching. Groups of males belonging to this stage seem apparent in the 1955 and 1956 Naden Harbour samples (Fig. 5H, I) and the May 16, 1956, sample of

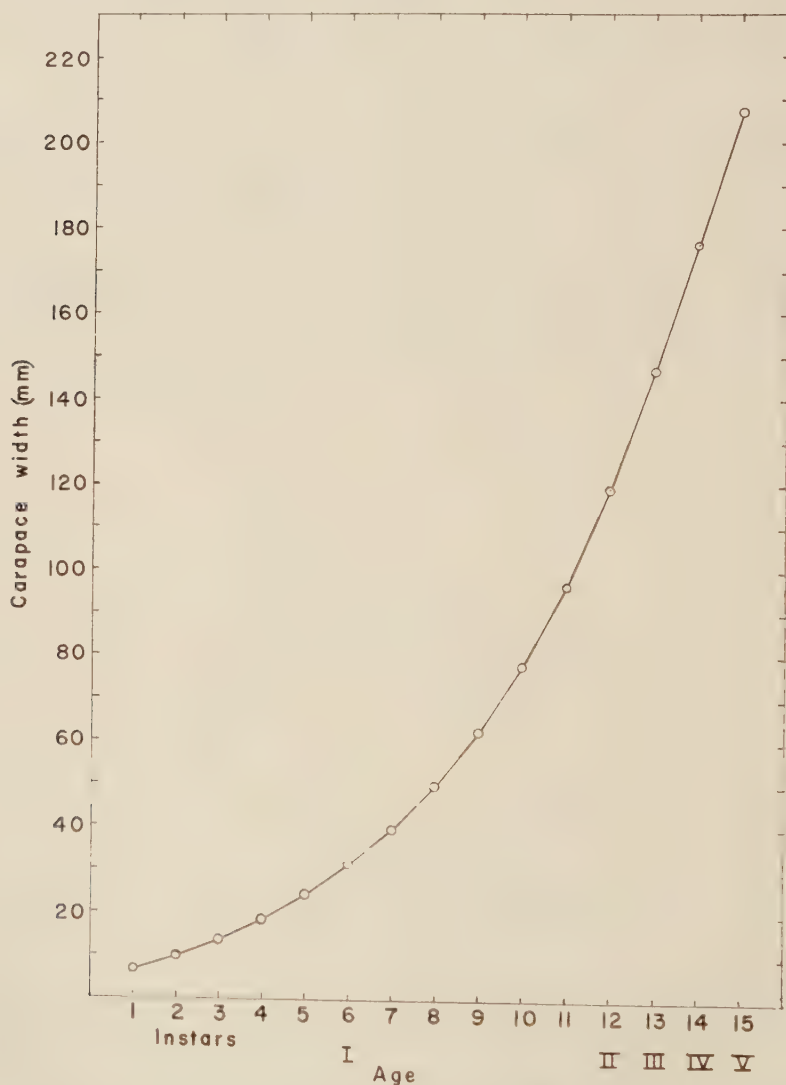


FIG. 10. Growth curve of male crabs.

the commercial catch from McIntyre Bay (Fig. 9). In this latter sample there is undoubtedly overlap between stages, but it seems likely that males of 200 mm and larger belong to stage 15. Probably most males spend about a year in stage 14, but tag recoveries indicate that some individuals may not moult for 2 years. The majority of males then seem to reach the 15th stage after 5 years, the rest after 6 or even 7 years. The estimated size of stage 16 is 241 mm but the largest male on record from the Queen Charlotte Islands measured 235 mm. Therefore, it is likely that stage 16 is rarely, if ever, attained and that stage 15 is in effect the final one in the crab's life. How long the crab lives after reaching the 15th stage is uncertain. Several large tagged males have been recovered after periods of freedom from 12 to 20 months, but the general lack of fouling on large male crabs seems to indicate that usually duration of the stage is no more than a year. Probably then males generally reach stage 15 after 5 years and live for a year longer; and even if moulting is less frequent in the latter stages, the maximum age is no more than 8 years.

In Figure 10 carapace widths of male crabs are plotted against stage number. An age scale in years is placed along the abscissa making the graph in effect a growth curve.

COMPARISON WITH EARLIER GROWTH STUDIES

In Table V present calculated stage sizes are compared with those determined earlier by MacKay and Weymouth (1935) and Cleaver (1949). All measurements of carapace width include the 10th antero-lateral spines. Cleaver's lengths for males and immature females were converted using an equation calculated from data of Weymouth and MacKay (1936):

$$Y = 0.0715X - 0.029$$

Y = combined length in cm of 10th antero-lateral spines; X = carapace width in cm exclusive of spines. Stage sizes of mature females were converted by taking spine lengths from the Fig. 9 in the same paper cited above.

The size of the first post-larval stage, 5.2 mm as given by MacKay and Weymouth, is lower than values of Cleaver and the present paper, between 5 and 7 mm and 6.9 mm, respectively. Also Waldron (1958) reported that 1st-stage crabs, moulting from the megalops, ranged from 6.6 to 8.3 mm. Thus it seems that the first 2 stages reported by MacKay and Weymouth should be combined so that the size range of stage 1 is between 5 and 8 mm. If their stage 3 at 9.7 mm is considered as stage 2, then it becomes comparable with Cleaver's 2nd stage at 9.4 mm and the 2nd stage here at 10 mm. Also, if successive stages are set back accordingly, then differences between stage sizes as found by Cleaver and by Mackay and Weymouth are not great, at least until after stage 12. That is, between stages 2 and 11 the stage sizes and increments determined by the latter workers are larger; stage 12 sizes differ by less than a millimeter; but in following stages the sizes and increments reported by Cleaver are somewhat greater. Thus

TABLE V. Comparison of average growth in width of carapace in male crabs from Queen Charlotte Islands with those obtained in Washington by Cleaver (1949). Measurements include 10th spines.

Washington			Queen Charlotte Islands		
Size	Crabs	Growth	Size	Crabs	Growth
<i>mm</i>	<i>No.</i>	<i>mm</i>	<i>mm</i>	<i>No.</i>	<i>mm</i>
21.0-30.6	25	6.4	29	1	8
74.5-84.2	6	19.9	80-84	1	24
85.3-94.0	19	21.5	85-89	3	24.4
			90-94	2	25.0
96.2-105.8	23	22.7	95-99	6	26.0
			100-104	2	22.0
107.0-116.7	51	22.7	105-109	3	27.6
			110-114	3	26.3
118.0-127.4	19	23.2	115-119	3	27.7
			120-124	2	27.0
128.6-138.4	8	24.7	125-129	7	28.4
			130-134	15	28.6
			134-139	11	29.2
139.6-149.1	6	25.3	140-144	22	30.4
			145-149	32	31.9
150.1-160.1	2	21.5	150-154	43	30.3
			155-159	53	29.4
161.2-171.0	1	24.0	160-164	43	29.4
			165-169	15	30.0

stage sizes as determined by these authors are similar if the assumption may be made concerning the grouping of the first two stages of MacKay and Weymouth. However, growth per moult and calculated stage sizes reported here for the Queen Charlotte Islands are larger than above values.

That actual increments reported here are larger seems attributable to the fact that moulting mostly occurred under natural conditions. Twenty-two males and 5 unsexed early post-larval crabs moulted in captivity. Twelve recovered tagged males moulted under natural conditions, and apparently the tag did not retard growth. The other male and all female records were obtained from crab traps. It might be argued that a trap constitutes an artificial surrounding, but it is obvious that crabs may enter freely and moult without the disturbances of being moved to a live-well or aquarium where water temperatures and salinity might differ.

MacKay and Weymouth tried to approximate natural conditions, but they state "... the increase of crabs in live-boxes was only about three-fourths of the normal among the smaller individuals". Practically no natural moulting records of larger crabs were obtained. Cleaver stated that only crabs which

moulted within a day after recapture were considered but Table V shows that, over approximately the same range, increments found here were larger than Cleaver's except in one group between 100 and 104 mm. Waldron (1958) obtained 102 moulting records (individuals less than about 32 mm, unsexed) in captivity at Newport, Oregon. He reports a similarity between these and Cleaver's data which is supported by his figure 13; but increments obtained at Newport are generally lower. Thus it seems reasonable to conclude that increments found in the course of earlier work were lower because moulting occurred mostly under artificial conditions. Kurata (1960) calculated growth equations for *C. magister* using data from MacKay and Weymouth, and I have calculated equations from Cleaver's moulting records. Constants of these equations are given in Table VI.

TABLE VI. Constants, a and b , of growth equations calculated from other authors.

	Juvenile		Male		Female	
	a	b	a	b	a	b
MacKay and Weymouth	1.1980	0.7068	1.1121	5.639	0.9343	22.735
Cleaver	1.23	0.57	1.02	20.6	0.849	34.03

For juveniles, constants shown above differ slightly, mostly in b values, from those calculated in equation (2); but the straight lines represented here are essentially similar. Cleaver's moulting juveniles included 130 unsexed individuals and males from 5.10 to 90.8 mm (converted values of class mid-points). The intercepts, or points of change in growth rate, determined from Cleaver's data, were 100.2 mm for males and 90.2 mm for females. These points approximate those calculate in this paper, but they differ appreciably from intersects (57.4 mm³ for males and 83.5 mm for females) derived from the data of MacKay and Weymouth. Kurata observes that the latter intercepts do not approach the size for attainment of maturity, about 100 mm, reported by these authors. Inspection of Kurata's figure 25C suggests that the intercept for males might be better placed at about 85 mm, and he does state that an inflexion at about 60 mm is not distinct. In any case, each growth study of *C. magister* has shown that growth rate does change at or near sexual maturity. And since line (2) and its intercepts with (3) and (4) are in fairly good agreement with those obtained from Cleaver's records, there is support for using its equation as a means of calculating growth by instars.

Ages determined here are much the same as those found by Cleaver. He concluded that age in years, from hatching, may be assigned to size as follows: after 1 year, 37.2 mm; after 2 years, 113.4 mm; after 3 years, 165.9 mm; and after 4 years, most males reached commercial size. However, according to Cleaver, 15 stages are required for attainment of commercial size as compared with the 14 stages estimated here.

³Reported by Kurata as 64.46 mm.

MacKay and Weymouth in their figures 5 and 6 show the following carapace widths (mm) of males at various ages:

<i>Age</i>	<i>Carapace</i>	<i>Age</i>	<i>Carapace</i>
1	10	5	115
2	60	6	130
3	85	7	150
4	100	8	165 (legal size, B.C.)

Their starting point for age determination is not stated clearly, but seems to be when fertilized eggs are extruded. In any case the discrepancy here is less than 6 months and cannot account for a growth rate only about half that of Cleaver's or our Fig. 10. However, there is evidence in MacKay and Weymouth's paper of a more rapid growth, at least for the first 2 years. They state that a sample collected in September (shown in their figure 3) contains 3 age groups: early post-larval stages or young of the year at 10 or 20 mm; yearlings at 40 to 70 mm; and 2-year-old crabs at 100 to 120 mm. These estimates contradict their main argument and conclusions concerning age determination, but agree reasonably well with Cleaver's and the present age estimates.

SUMMARY

1. Data are presented on growth of the Pacific edible crab and an attempt is made to estimate age of crabs in the Queen Charlotte Islands region.
2. A total of 2,820 early post-larval crabs were collected by small-meshed trawl from 1953 to 1956 in McIntyre Bay and Naden Harbour.
3. Five post-larval unsexed crabs moulted; increments of carapace width were from 36.3 to 46.5%. In a sample of 1,175 unsexed crabs, modes at 6.9 and 10 mm were identified as 1st and 2nd instars, respectively.
4. Moulting records of larger crabs were obtained as follows: from 1953 to 1957, 250 males and 44 females moulted in crab traps; in 1956 and 1957, 22 males moulted in live-wells; and between 1955 and 1959, 12 tagged males moulted while at large. Size range of moulting males was from 83 to 186 mm; females from 88 to 145 mm.
5. For each sex, carapace widths of early post-larval and larger crabs before moulting were plotted on arithmetic scale against carapace widths after moulting, to produce straight lines. Using equations of these lines and size of the 2nd stage, average carapace widths were calculated for stages 3 to 16.
6. In width frequency distributions of 8,145 crabs separation of stages was sufficient for identification of age groups. From seasonal occurrence of groups and indication of moulting frequency from tag recoveries, it is estimated for male crabs that a year after hatching stage 5 or 6 is reached; after 2 years stage 11 or 12 is attained; after 3 years most crabs are in the 13th stage; after

4 years stage 14 is reached; and generally at the end of 5 years crabs are in stage 15. Growth of females appears similar for the first 2 years but afterwards is slower.

7. Both sexes reach sexual maturity in the 11th or 12th stages after 2 years. Males reach commercial size in stage 14 after 4 years. Probably the maximum age of crabs is 8 years.

ACKNOWLEDGMENTS

The writer wishes to acknowledge the assistance of Messrs R. G. Helbecque and D. M. Lawless, who measured many moulted crabs and carried out tagging experiments. Drs K. S. Ketchen and W. E. Ricker read the manuscript and offered suggestions. Mr Shoichi Tanaka kindly translated sections of the paper by H. Kurata.

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APPENDIX TABLE A. Carapace widths of post-larval crabs, McIntyre Bay, August 29 to September 9, 1953.

<i>mm</i>	<i>No.</i>	<i>mm</i>	<i>No.</i>	<i>mm</i>	<i>No.</i>	<i>mm</i>	<i>No.</i>	<i>mm</i>	<i>No.</i>
5.8	1	8.1	2	10.4	35	12.7	1	15.0	1
.9	2	.2	0	.5	25	.8	1	.1	0
6.0	5	.3	1	.6	36	.9	1	.2	1
.1	6	.4	0	.7	26	13.0	1	.3	1
.2	16	.5	0	.8	26	.1	0	.4	0
.3	13	.6	2	.9	18	.2	2	.5	0
.4	29	.7	2	11.0	11	.3	7	.6	0
.5	40	.8	1	.1	10	.4	3	.7	3
.6	43	.9	3	.2	5	.5	3	.8	0
.7	36	9.0	11	.3	10	.6	1	.9	1
.8	67	.1	7	.4	3	.7	2	16.0	0
.9	74	.2	7	.5	7	.8	0	.1	1
7.0	63	.3	8	.6	7	.9	1	.6	1
.1	50	.4	11	.7	1	14.0	2	18.3	1
.2	34	.5	14	.8	2	.1	7	.5	1
.3	28	.6	19	.9	1	.2	2	19.5	1
.4	24	.7	27	12.0	1	.3	1	.8	1
.5	5	.8	27	.1	1	.4	3	20.1	1
.6	5	.9	35	.2	0	.5	2	.7	1
.7	2	10.0	32	.3	1	.6	3	21.0	1
.8	2	.1	41	.4	1	.7	1	.4	1
.9	1	.2	30	.5	1	.	1		
8.0	0	.3	32	.6	0	.9	1		

APPENDIX TABLE B. Moulting records of tagged male crabs, released during 1955, 1956 and 1957 and recovered in 1956, 1957, and 1959.

Carapace width		Increment	
Old	New		
<i>mm</i>	<i>mm</i>	<i>mm</i>	%
144	178	34	23.6
146	178	32	21.9
155	180	25	16.1
158	174	16	10.1
159	190	31	19.5
160	174	14	8.8
163	193	30	18.4
164	193	29	17.7
165	193	28	17.0
168	200	32	19.1
172	202	30	17.4
172	203	31	18.0

APPENDIX TABLE C. Records of male crabs moulting in live-wells at Masset, 1956 and 1957

Carapace width		Increment	
Old	New		
<i>mm</i>	<i>mm</i>	<i>mm</i>	%
1956			
83	107	24	28.9
92	115	23	25.0
98	124	26	26.5
105	135	30	28.6
115	140	25	21.7
133	164	31	23.3
136	163	27	19.9
147	174	27	18.4
160	186	26	16.3
160	188	28	17.5
167	199	32	19.2
174	201	27	15.5
1957			
97	121	24	24.7
103	124	21	20.4
110	138	28	25.5
129	153	24	18.6
131	154	23	17.6
131	160	29	22.1
132	159	27	20.5
136	164	28	20.6
150	179	29	19.3
160	188	28	17.5

Proximate Composition of Canadian Atlantic Fish. III. Sectional Differences in the Flesh of a Species of Chondrostei, one of Chimaerae, and of Some Miscellaneous Teleosts¹

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ABSTRACT

Proximate analyses of sections of the flesh of several teleosts and also of a sturgeon and a chimaera are reported. Among the teleosts the proximate composition of the white meat is very similar, with the exception of the fat, which varies from 0.7% in the lean species such as haddock to 12% in the spiny eel. Protein (protein N $\times$ 6.25) ranges from 14.8 to 16.2% for most species, but is lower in the sturgeon and chimaera, while the previously reported values for mackerel, tuna and halibut are higher. The belly flap tissue is only slightly more fatty than the white meat in haddock and the white sucker, in contrast to the high values for halibut and mackerel. The brown lateral layer contains about 2% lipid in haddock and wolffish with much higher values in other species; its non-protein N content is similar to that of the white meat for the most part. Although present only in traces in some species, the brown lateral layer makes up about 8% of the flesh of the tail section of the haddock, but only 1% of the middle section.

INTRODUCTION

PREVIOUS PAPERS in this series (Mannan *et al.*, 1961a,b) have dealt with the variation in composition of the different sections of the edible portion of halibut, mackerel, tuna and swordfish. In order to gain a picture of the variation over a range of fish species, further work on several species of teleosts, including haddock, cod, rosefish, spiny eel, shad, and the white sucker is now reported. Because of their taxonomic position between the elasmobranchs and teleosts, a sea sturgeon and a chimaera are also included.

A few studies on the Pacific salmon have been reported. Thurston (1958) studied the variation in moisture, fat, protein and ash in various sections of Alaska pink salmon (*Oncorhynchus gorbuscha*), and similar results were obtained by Thurston and Groninger (1959) in Puget Sound pink salmon. The steak section of the Alaska samples, including the dark meat, averaged higher in fat content at the nape, 4.8%, than in the caudal section, 2.6%, with intermediate values in the centre, 3.5%. The fat content of the fatty tissue around the dorsal fin, of the brown lateral layer and of the belly flap was much higher and more variable, averaging 15.7, 12.5 and 9.5% respectively; light meat averaged 2.1%. Thurston also concluded that variation with sex and size was small in comparison with that due to sexual maturity, agreeing with the much earlier work of Dill

¹Received for publication March 17, 1961.

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(1921). Some of these changes have also been studied recently in sockeye salmon (*Oncorhynchus nerka*) by Idler and Bitners (1958).

A thorough study of the fat and water distribution in the musculature of Atlantic herring (*Clupea harengus*) was carried out in Germany by Brandes and Dietrich (1953). The belly-flap muscle gave very high lipid values, about 47% as compared to values of 23 to 27% for the muscle at the anterior end of the fillet, 27 to 31% at the thickest part, and 14 to 18% at the caudal end of the fillet. Fat and moisture were found to be closely related.

EXPERIMENTAL

SOURCES OF SPECIMENS AND SAMPLING

The species are classified according to the American Fisheries Society (1960) and Jordan and Evermann (1896) as follows:

Class CHONDRICHTHYES

Order CHIMAERIFORMES (CHIMAERAE) *Hydrolagus affinis*—chimaera

Class OSTEICHTHYES

Order ACIPENSERIFORMES (CHONDROSTEI) *Acipenser oxyrhynchus*—
Atlantic (sea) sturgeon

Order CLUPEIFORMES (ISOSPONDYLI) *Alosa sapidissima*—
American shad
Clupea harengus harengus—
Atlantic herring

Order CYPRINIFORMES (OSTARIOPHYSI) *Catostomus commersoni*—
white sucker

Order NOTACANTHIFORMES (HETEROMI) *Notacanthus nasus*—spiny eel

Order GADIFORMES (ANACANTHINI) *Gadus morhua*—cod
Melanogrammus aeglefinus—
haddock

Order PERCIFORMES (PERCOMORPHI) *Sebastes marinus*—rosefish
Anarhichas lupus—wolffish
(Atlantic)

Two specimens of *spiny eel* were obtained through the courtesy of Mr George Sullivan of this Board's office in Halifax. They were caught at 120 fathoms near Green Bank; one was 51 cm long (December 1960), and the other 112 cm (January 19, 1961). Samples of the white dorsal meat at the thick part of the fish (A) were taken. Only a trace of brown lateral-line tissue was present, but in the larger fish there was a layer of white fat (blubber, FL) about 1.3 cm thick at the dorsal line. This extended around the belly as a thin layer under the skin, comprising one-fifth of the weight of the flesh of a cross-sectional steak at the thick portion of the fish.

The minced mixed fillets (M) of a *shad* 32 cm long, caught by net near Halifax on November 2, 1960, were analyzed.

Several specimens of *white sucker*, all 43 cm long, were netted in a river (Halifax County) on May 28, 1959. Samples of the flesh from sections A, B (tail section, white meat), and C (belly flap) (Mannan *et al.*, 1961a) from two fish were minced and mixed for analysis. Similar samples were taken from two fish stored for 3 months at -23°C . No trace of brown lateral-line flesh was observed.

The *sturgeon*, measuring 80 cm long, was caught in salt water in St. Margaret's Bay on April 30, 1954, and was alive prior to sampling (Dingle and Dyer, 1955).

The *chimaera*, 118 cm long, was a ripe female caught on November 19, 1960, off St. Pierre Bank at 300 fathoms. The thick white dorsal muscle was analyzed in both these specimens.

The *haddock*, market size, were caught in Terence Bay, near Halifax, on April 20, June 6 and July 24, 1959. The first lot was frozen (in polyethylene bags) and stored for 2 months at -23°C , while the other two lots were sampled while still in the pre-rigor state (iced). Samples of the white meat were taken between myotomes 7 and 14 at the thick part of the fish (A); sample B included the fillet portion from the tail almost to the vent, while sample C was the belly flap, which was not included in A. In the June 6 lot, a section L, midway between the nape and the tail was also taken.

The May 28, 1959, sample of *cod* (lot I, Table III) was taken live from the fish-holding tank at the laboratory.

A *wolffish*, 74 cm long, was caught on February 6, 1960, and brought in alive from the Banks by the Board's research vessel *A. T. Cameron*.

For comparison purposes, the average composition of cod and rosefish fillets from previously reported frozen storage experiments are included in Table V.

The *cod* samples were of minced, mixed lots of fillets (M) from commercial market-size fish. Lot II samples were from cod caught off Sable Island on July 12, 1955, iced 2 days on a trawler (Dyer, Fraser, Ellis and MacCallum, 1957); lot III from a July 26, 1956, catch also off Sable Island, landed after 2 days in ice (Dyer, Fraser and MacCallum, 1957); lot IV from Western Bank, October 25, 1956, landed after 1 day in ice on a trawler; lot V from Quero Bank, October 18, 1957, landed after 8 days in ice (Dyer and Fraser, 1959); lot VI from off Sable Island, September 13, 1957, landed after 4 days in ice. The fillets had been frozen in commercial 1-lb blocks with machine-sealed, waxed paper overwrap, and were stored at either -18°C or at -23°C . Samples were periodically removed, cut into small pieces with a knife and well mixed, while the flesh was still hard frozen, to avoid loss of any drip that might be formed on thawing. There was no change in any of the values reported during storage of these frozen lots.

The *rosefish*, lot VII, was from a lot landed by trawler on November 13, 1952.

TABLE I. Composition of edible portions of miscellaneous teleosts, Chondrostei, Chimacrae. All values are on wet-weight basis. Crude protein calculated from total N $\times 6.25$; protein from protein N $\times 6.25$. Total S₁ is sum of water, lipid, ash and crude protein; total S₂ is sum of water, lipid, ash and protein. (A—thick section, white meat; B—tail section, white meat; C—belly flap; M—minced mixed filets; FL—white fatty blubber.)

Miscellaneous teleosts	Section	Water	Lipid	Ash	TN	Crude protein	Total S ₁	NPN	PN	Protein	Total S ₂	TMA	TMAO	SPN	AM	Alb	FFA	NPN
		%	%	%	%	%	%	%	%	%	%	mg N/100 g	mg N/100 g	---	% TPN	---	% lipid	% TN
HETEROMI Spiny eel Dec. 1960 Jan. 1961	A	73.5	5.4	...	2.99	18.7	...	0.40	2.59	16.2	...	2.2	78	...	...	...	...	13.4
	A	67.5	12.2	1.07	2.65	16.6	97.4	0.40	2.25	14.1	94.9	0.3	98	...	...	...	...	15.1
	FL	31.1	56.0	0.52	1.21	7.6	95.2	0.20	1.01	6.2	93.9	0.3	41	...	...	...	...	16.5
	M	72.9	17.2	...	2.92	18.3	...	0.37	2.56	16.0	...	1.8	30	...	...	...	...	12.7
ISOSPONDYLI Shad Nov. 1960	A	80.6	1.1	1.30	2.80	17.5	100.5	0.40	2.40	15.0	98.0	0.1	0.1	98	74	24	2.0	14.3
	B	80.8	2.0	1.20	2.92	18.3	102.2	0.40	2.51	15.7	99.7	...	...	...	...	...	2.6	13.7
	C	80.0	0.9	1.50	2.78	17.4	99.8	0.40	2.38	14.9	97.3	...	...	...	...	...	3.2	14.4
	A	81.9	1.4	1.30	2.65	16.6	101.1	0.34	2.31	14.4	99.0	...	...	91	67	24	10	12.8
OSTARIOPHYSI White sucker May 1959, (Av. of 2 fish)	B	81.5	1.1	1.30	2.65	16.6	100.4	0.36	2.29	14.3	98.2	...	...	89	69	20	11	13.6
	C	81.3	1.3	1.50	2.53	15.8	99.9	0.34	2.19	13.7	97.8	...	...	...	...	...	10	13.4
	A	77.8	6.2	...	2.27	14.2	...	0.34	1.93	12.1	...	0	0	...	...	...	...	15.0
	M	83.4	0.7	...	2.90	18.1	...	1.36	1.54	9.6	...	0.4	234	...	...	...	...	46.9
CHONDROSTEI Sea sturgeon Apr. 1954	A	77.8	6.2	...	2.27	14.2	...	0.34	1.93	12.1	...	0	0	...	...	...	...	15.0
	M	83.4	0.7	...	2.90	18.1	...	1.36	1.54	9.6	...	0.4	234	...	...	...	...	46.9
CHIMACRAE Chimaera Nov. 1960	A	77.8	6.2	...	2.27	14.2	...	0.34	1.93	12.1	...	0	0	...	...	...	...	15.0
	M	83.4	0.7	...	2.90	18.1	...	1.36	1.54	9.6	...	0.4	234	...	...	...	...	46.9

ANALYTICAL PROCEDURES

The analytical procedures are given in Part I of this series (Mannan *et al.*, 1961a). Values in Tables I and III of the present paper for total nitrogen (TN), non-protein nitrogen (NPN), trimethylamine oxide (TMAO), trimethylamine (TMA), salt-peptizable protein (SPN) and actomyosin (AM), are the average of duplicate determinations.

RESULTS AND DISCUSSION

SPINY EEL

The spiny eel was a fatty fish, 5.4 to 12.2% lipid in the white flesh (Table I), with the other constituents having values similar to those in the other teleost fishes analyzed. The fatty "blubber" tissue in the larger specimen contained 56% lipid, but only 6.2% protein (protein N $\times$ 6.25) in agreement with the reduced moisture content of 31%. NPN, ash, and TMAO were also correspondingly lower.

SHAD

The shad, having 17.2% lipid but a normal protein content of 16%, was a fall specimen in good condition. Clark and Almy (1918) also reported high lipid values for shad prior to the spawning migration in April, whereas in the spawning or spent fish in May and June the fat was reduced to 3 to 6%, with a slight lowering of protein as well. Herring belong to this family, and Leim (1958) found fat values as low as 1.2% in April and June, with values as high as 27.5% in August to November in the Bay of Fundy. Here, spawning occurs mainly in the late fall (Tibbo and Legaré, 1960).

WHITE SUCKER

The white sucker was a non-fatty fish, with no dark muscle, and showed almost no variation between the thick muscle A, the tail portion B, or the belly flap C. Other values were almost identical with those of haddock and cod, except for the absence of TMAO. There is a possibility that the fat may have been depleted by spawn formation and samples taken earlier in the season should be examined. Protein extractability was only slightly less after frozen storage for 3 months at -23°C .

STURGEON AND CHIMAERA

The sturgeon was medium-fatty, containing about 6% lipid. The moisture content was rather high and protein was rather low, being only 12.1%. The chimaera, on the other hand, being more closely allied to the elasmobranchs, was quite different; its lipid and protein contents were very low, 0.7 and 9.6% respectively, while the moisture content was high, 83.4%. In this respect, it would be interesting to determine whether this was related to the spawning

condition or was characteristic of this species. According to Vinogradov (1953), no analytical data have been reported for this Order. About 47% of the total nitrogen was NPN, and the TMAO was also very high, 234 mg N per 100 g. The latter compares with the value of 180 found in the Pacific species (*Hydrolagus collieri*) (Norris and Benoit, 1945), and with the high TMAO and urea contents in the elasmobranchs (Dyer, 1952; Groninger, 1959).

HADDOCK

In haddock, a thin layer of dark fatty tissue, much less pronounced than in mackerel, is present under the skin along the sides of the fish and thickens towards the tail. Dissection showed that it comprised 8% of the edible tissue in the tail section, but only 0.8% in the cross-section at the thick part of the fish (Table II).

TABLE II. Proportion of skin, bone and edible meat in steaks from a haddock 64 cm long, landed very fresh, probably no more than 1 to 2 days on ice, on Feb. 1, 1961.

	Steak A (thick section; total weight 396 g)	Steak B (tail section; total weight 166 g)
	%	%
Proportion of total weight:		
Skin	5.8	6.0
Bone	10.4	9.0
Fins	4.0	9.6
Edible portion	79.8	75.4
Proportion of edible portion:		
White meat	82	92
Dark layer	0.8	8
Belly flap	17	0

The belly flap comprised about 17% of the edible portion of the latter. The lipid content of the brown lateral line tissue was 2% (Table III) and thus the B section (including dark meat) should have been slightly higher in lipid, but the differences were much smaller than in halibut and the fatty species. The belly flap of the various samples was somewhat higher in lipid, 0.89%, as compared to averages of 0.71 and 0.77 in the A and B sections. Little difference appeared in protein, moisture or in NPN between the various sections. Comparable data for average values reported by various authors (Table IV) agree closely, except for fat content, which depends on the method used (Mannan *et al.*, 1961a). The proportion of the total nitrogen contributed by NPN, 16%, was slightly higher than in the halibut, but lower than in the mackerel family. Komarov (1932) found an NPN content of 0.38%, which is slightly less than that found here, 0.45% (wet weight).

An increase in moisture content during June to July was not found in the present samples, although Crooks and Ritchie (1939) noted an increase from the

yearly average of 81.0% to values of 84.1% in May and 82.7% in July. This corresponds to the spawning period, which, according to Homans and Vladykov (1954), is mainly in April and May in the Canadian Atlantic area. These authors also state that haddock do not feed during the period just prior to or during spawning. In starving cod held 78 days in a tank at about 14°C, the

TABLE IV. Proximate composition of edible flesh of haddock (wet-weight basis; crude protein calculated from total N $\times$ 6.25).

Source of data	Water	Lipid	Ash	Crude protein
	%	%	%	%
Crooks and Ritchie (1939)	79.3–84.1	0.09–0.27	Av. 1.24	...
	Av. 81.0	Av. 0.13	—	...
McCance and Widdowson (1940)	81.3	0.6	...	15.9
Reay <i>et al.</i> (1943)	79.1–84.1	0.1–0.6	...	14.6–20.3
Watt and Merrill (1950)	80.7	0.1	1.4	18.2
Braekkan (1958)	78.6	0.25	1.1	19.7
Average A and B (Table III)	80.5	0.74	1.20	18.3

moisture increased from about 80 to between 84 and 88% (Love, 1958). Thus, the utilization of protein and its replacement by water in the final stages of the maturation period, when the fish are fasting as well, may be greater in these species than in those with fat reserves. Even in salmon, a considerable proportion of the energy requirements for maturation is supplied by the body protein in addition to that derived from the fat reserves (Idler and Bitners, 1958). These authors also show that the protein and fat lost are only partially replaced by a gain of water in the flesh. A few analyses of cod showed protein, fat and water percentages almost identical to those in haddock, and no gross difference was found between the various sections.

WOLFFISH

The sample of wolffish flesh gave values almost identical to those of haddock, except that the white flesh had 2.1% fat. Only a very thin yellowish fatty layer along the lateral line was present in this species, and an excised sample contained only 2.6% lipid. The 0.40% NPN value was higher than that (0.26%) reported by Shewan (1951).

COD

Some analyses for minced, mixed fillets (M) from commercial market-size cod are summarized in Table V. Moisture, lipid, protein, and soluble protein nitrogen values are almost identical to those of haddock, with NPN being a bit lower and TMAO higher. It is interesting to note that the average protein found in cod, 15.6%, agreed well with the value of 15.2% obtained by Dambergs (1959) by an extraction procedure not involving nitrogen estimations.

TABLE V. Summary of composition of cod and rosefish fillets from frozen storage experiments. Average values (wet-weight basis) are given, together with the standard deviation in parentheses, followed by the number of samples analyzed.

Sample	Water		Lipid	Crude protein		NPN		PN		Protein	TMA		TMAO	SPN	Alb	NPN
	%	%		%	%	%	%	%	%		mg N/100 g	% TPN				% TN
Cod: Jul. 12/55, M iced 2 days	80.6 (±0.55)	...	...	2.83 (±0.056)	47	17.7	0.35 (±0.02)	2.48 (±0.06)	47	15.5	0.97 (±0.34)	23	59.8 (±8.2)	92	23	12.3
	81.7 (±0.63)	...	...	2.80 (±0.045)	16	17.5	0.31 (±0.018)	2.49	—	15.6	1.1 (±0.42)	20 (±2.0)	61.7 (±9.3)	83 (±2.5)	8	11.1
Oct. 25/56, M iced 1 day	81.6 (±0.76)	...	...	...	...	...	...	...	...	...	0.5	23	75	86	—	...
Oct. 18/56, M iced 8 days	81.3 (±0.45)	...	...	...	...	...	...	...	...	...	6.0	22	78	86	22	...
Sept. 13/57, M iced 4 days	81.4 (±0.44)	0.59 (±0.074)	81	...	...	...	...	...	...	...	0.70 (±0.21)	12	...	91	23	...
Rosefish: Nov. 13/52 M	79.6 (±0.63)	3.3* (±0.92)	14	2.80 (±0.077)	11	17.5	0.31 (±0.055)	2.49	—	15.6	4.0	20	...	83	20	11.1

*Crude fat by acid hydrolysis (A.O.A.C., 1955). Fat by $\text{CHCl}_3\text{-Na}_2\text{SO}_4$ (Dyer and Morton, 1956) is 2.0 (±0.63) 18.

ROSEFISH

Previous analyses of rosefish (Dyer *et al.*, 1956) showed a fat content averaging about 3.3% (Table V), but otherwise the composition was identical to haddock.

TABLE VI. Proximate composition (on wet-weight basis) of various members of the cod family. Percentages of crude protein calculated from total N $\times$ 6.25. (Data from Braekkan, 1958.)

	Water	Lipid	Ash	Crude protein
	%	%	%	%
Cod— <i>Gadus morhua</i>	80.4	0.34	1.1	18.1
Coalfish— <i>Gadus virens</i> (= American pollock— <i>Pollachius virens</i>)	78.4	0.7	1.2	19.4
Pollack— <i>Gadus pollachius</i>	77.7	0.6	1.6	19.1
Haddock— <i>Gadus aeglefinus</i>	78.6	0.25	1.1	19.7
Ling— <i>Molva molva</i>	78.5	0.32	1.5	19.2
Cusk— <i>Brosius brosme</i>	77.8	0.25	1.5	19.8

The similarity of composition of the members of the Orders Anacanthini and Percomorphi is striking, the exception being the fat and the TMAO values. This is also evident in the data of Braekkan (1958), summarized in Table VI, which include other closely related species. It appears that there is very good agreement in samples from various parts of the world.

COMPARISON OF COMPOSITION OF THE SECTIONS OF ABOVE VARIOUS SPECIES WITH THOSE OF HALIBUT, MACKEREL, TUNA AND SWORDFISH (Mannan *et al.*, 1961a,b)

Fat. The white meat varied from about 0.7% in haddock and similar lean fish to about 6.5%, except for mackerel which reached 16%. The flesh of the belly flap had a much higher lipid content in the halibut and mackerel group. The reddish-brown lateral layer was also much richer in lipid than the white meat, ranging from about 2% in haddock, 4 to 8% in halibut to about 22% in mackerel.

Moisture. This varied from 74.2 to 83.4% in the white muscle, except in fat mackerel where it was only 64%. It was lower in the belly flap and dark meat, where fat was higher.

The sum of moisture and lipid varied between 77.5% and 82%, except for the belly flap of the fat mackerel with 37.2% fat, where the sum was 86.5%, and the sturgeon and chimaera, where it was 84 and 84.1%. In the latter, the protein was also much lower, about 9 to 12%.

Total nitrogen. This ranged from 2.8 to 3.6%, except for a value of 2.3% in the sturgeon, while protein had a very narrow range of 14.8 to 16.2% for most species. It was higher in the halibut, mackerel and tuna, lying between 18.9 and 19.5%, and lower in the sturgeon and chimaera, with only 12.1 and 9.6% as noted above. Both total nitrogen and protein were lower in the belly flap and in the dark brown lateral line muscle, indicating that in these fatty tissues some protein as well as moisture is displaced by fat.

Non-protein nitrogen. NPN varied from 0.31 to 0.46%, but was higher in the mackerel and swordfish families, 0.58 to 0.73%, and very much higher in the chimaera, 1.4%. As a proportion of the total nitrogen, it ranged from 11 to 16%, with values of 19 to 20% for tuna and swordfish and 47% for chimaera. Except for a high value in the belly flap of the halibut, there was little difference between the white, dark or belly flap meat. TMAO was lower in the belly flap muscle of halibut, haddock, and mackerel, but higher in the brown muscle of the latter. These data confirm and extend Shewan's results (1951), which ranged from 9 to 14% (of total N) in the flatfish and gadoids, and 14 to 18% in the herring group with much higher values (34 to 38%) in the elasmobranchs.

Protein extractability. This was generally 90 to 97%, with lower values for the belly flap and dark brown muscles. The non-actomyosin fraction or "albumin", soluble at low ionic strength, appeared to be very constant, 20 to 23%, except for one species, the tuna, where it was 31% of the protein nitrogen.

Free fatty acid (FFA). These values in the very fresh fish ranged from 0.2 to about 5% of the extracted fat. They appeared to be lower in the more fatty samples, probably because the acid phospholipid components contribute a large proportion of the acidity in the lean fish where phospholipid makes up half or more of the total fat (Olley and Lovern, 1960; Bligh, 1961), whereas in the fatty species the constitutional lipid is effectively diluted by the large amounts of triglyceride present (Dill, 1921). In those few samples which were stored frozen for 2 to 3 months prior to analysis, large increases in free fatty acid occurred in the white sucker and haddock, but little if any increase was observed in halibut or mackerel. It appears that hydrolysis, presumably enzymic, occurs in the lipid of the haddock and the white sucker, as it does in cod (Dyer and Fraser, 1959).

Proportion of brown lateral-line tissue, and other fatty tissues. In the mackerel, the brown fatty layer accounted for about 14% of the weight of the edible part, in halibut about 6 to 7%, in haddock about 8% in the tail section and only 1% in the thick part. It was also prominent in the tuna and swordfish. Only a trace was present in the wolffish, spiny eel, chimaera and white sucker.

A layer of blubber or white fatty tissue, about two-thirds fat, was present in some specimens, e.g. tuna and the large spiny eel. It was thickest around the dorsal fin and appeared as a separate layer enclosed in connective tissue beneath the skin, and was separate from the brown fatty lateral-line tissue.

These results show that while the average composition of most of the species of fish discussed is very similar and varies little with season or area, in others there is a great variation, not only with season or maturity, but in the different sections of the individual specimens. To compare the nutritional value, the composition of the white meat should first be considered; then, if any considerable portion of the dark meat or other fatty parts will be included in the actual portion consumed during a meal, the calculation should be adjusted accordingly.

Note added in proof:

It has been brought to our attention that Braekkan (1959) has provided a good description of the occurrence of red muscle in several fish species, and suggests that the red muscle provides a storehouse for fat, glycogen and other metabolites in close proximity to the white or ordinary muscle. The position and amount of the red muscle varies from the anterior to the caudal ends of the fish and the arrangement in the tuna and shark families was found to differ considerably, being present as a distinct muscle embedded in the main trunk muscle rather than being situated under the skin along the lateral line as in most species. The fat content of the red meat was higher by 1.5 to 7 times that of the ordinary muscle in the species examined, in agreement with the present results.

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Oceanographic Features of Inlets in the British Columbia Mainland Coast¹

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¹Received for publication May 15, 1961.

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ABSTRACT

The inlets of the British Columbia mainland coast are morphologically fjords but few possess sills of depth less than 15 m.

The most significant influence in them is the fresh water runoff, chiefly from rivers. It is large in many of the inlets fed by rivers from glaciers, is seasonal in flow, and determines the estuarine character and circulation of the inlets and thereby the distribution of water characteristics.

In the large-runoff inlets the surface salinity increases from zero at the head to coastal sea values at the mouth. In winter the surface temperature is low and uniform but in summer it increases from the head, reaches a maximum where the salinity is about 8‰ and then diminishes toward the mouth. The water is highly stratified, particularly from the surface to about 20 m depth where the salinity rises to 90‰ or more of the deep water value. The marked halocline in the upper layer is accompanied by a marked thermocline. Below 50 m the salinity and temperature do not change much along the length of an individual inlet.

There is a pronounced geographical change of deep water characteristics from 30.7‰ and 8.3°C in the southern to 33.2‰ and 6.3°C in the northern inlets. In general, seasonal changes of temperature can be detected to 100 m but of salinity to only 30 m, suggesting a difference in the rates of eddy diffusion. Changes of deep water characteristics occur irregularly.

In many of the inlets a temperature minimum at 20 to 100 m depth is common in the inner reaches in the spring and diminishes in intensity later in the year.

In the inlets with medium or small runoff the surface salinity is generally higher and changes less along an inlet, and the halocline and thermocline are less marked. The homogeneous surface layer characteristic of the large-runoff inlets is usually absent.

Generally the large-runoff inlets show less variable dissolved oxygen values along an inlet at any depth than do the small-runoff inlets. Supersaturation of the upper layers is common, and there is often an oxygen maximum just below the halocline of the larger-runoff inlets. A few small-runoff inlets have a mid-depth oxygen minimum in which the lowest values are at the inlet head. Dissolved oxygen values of less than 2 ml/l are not common in any mainland inlets and zero values have not been definitely recorded.

The optical turbidity in large-runoff inlets is high in the surface layer, lower in the main body of water, and often increases in the bottom 50 to 100 m. At the heads of the large-runoff inlets Secchi-disc depths of 0.1 to 0.3 m are common in the summer. In the inlets with smaller runoff the turbidity is less. In both types the turbidity is at a maximum in the summer and a minimum in the winter, and the particulate material in the water is largely minerogenic.

Internal waves of period 1 to 4 minutes and amplitude up to 5 m occur in the upper layers. At mid-depth (20 to 150 m), vertical oscillations of the isotherms with semidiurnal tidal period are common, the amplitude being from 5 to 75 m.

A waxy substance sometimes found floating or washed ashore in Bute Inlet during cold winters appears to be peculiar to that inlet as no reference has been found to any similar substance being observed elsewhere in the world.

1. INTRODUCTION

THE MAINLAND COAST of British Columbia is indented by many long, relatively narrow, deep bodies of water opening on to the sea at one end and generally having a river at the other. These indentations are variously and unsystematically named "inlet", "arm", "channel", "canal", etc. on the charts. For simplicity, and following the practice of Vancouver (1798) who was the first to present a systematic description of the coast, the term "inlet" will be used as a generic term in the present discussion. The appellation "inlet", "canal", etc. will generally be omitted when referring to inlets by name.

An outline of the coast is given in Fig. 1 and 2 in which the more important inlets are named. There are 42 inlets (named in Table I) of 10 (nautical*) miles (18.5 km) or more length in the mainland coast, and in addition 15 in Vancouver Island and one in the Queen Charlotte Islands.

Their shape and location and the inflow of fresh water which gives rise to a brackish surface layer identifies most of these inlets as estuaries in the sense in which the term is currently used to describe a "semi-enclosed body of water having a free connection with the open sea and containing a measurable quantity of sea salt" (Pritchard, 1952, p. 245). The considerable depth and other characteristics of the British Columbia inlets suggest a comparison with the fjords of the Norwegian and New Zealand coasts and the deep inlets on the Pacific coast of South America, and a distinction from shallow estuaries such as Chesapeake Bay. It will be made clear however that there are some significant differences from the Norwegian fjords.

The investigation of estuarine circulation has attracted considerable attention in recent years and the Institute of Oceanography of the University of British Columbia has selected as one problem the study of the circulation in these deep estuaries.

Before the commencement of the present study, Alberni Inlet in Vancouver Island had been studied in detail by Tully (1949), and a limited amount of information, chiefly for the surface layers, was available for several others. These included Indian Arm, Howe Sound and Bute Inlet (Hutchinson and Lucas, 1931), Howe Sound, Jervis, Sechelt and Toba Inlets (Carter, 1932, 1934) in the mainland, and Saanich (Carter, 1934) and Nootka Sound (including Muchalat, Tlupana and Tahsis Inlets) (Tully, 1937) in Vancouver Island. The remainder of the inlets were unexplored oceanographically in 1950. As it was not possible to study all of the inlets in detail it was necessary to make some selection. To assist in this selection and to guide theoretical studies it was therefore necessary to extend the data to determine what characteristics were common to this type of water body and independent of local influence such as shape, wind stress etc. Since the study of the dynamics of the estuarine circulation was to be the salient feature it was appropriate to examine the inlets during the early summer when the fresh water run-off from the rivers was at its maximum.

*All sea distances given in this paper are in nautical miles.



FIG. 1. British Columbia mainland coast, northern portion, showing main inlets.



FIG. 2. British Columbia mainland coast, southern portion, showing main inlets.

To provide the general cover, an extensive 3-month cruise to 21 of the inlets was made in 1951. Most of the other mainland inlets were visited between 1952 and 1960. In addition, several of the typical southern inlets were visited a number of times between 1951 and 1960. Most of the cruises were made in the spring or summer, but some year-round data are available for Bute (1950-52; Tabata and Pickard, 1957), Bute and Jarvis (1957-58), and Indian (1956-60; Gilmartin, 1960). The detailed data are available in the form of Data Reports, Institute of Oceanography, University of British Columbia (1953-1960) for the individual cruises.

The object of the present paper is to provide a summary of some of the oceanographic characteristics of the British Columbia mainland inlets, for reference and for comparison with similar coastal areas, and to draw attention to particular aspects of the inlet characteristics and of problems associated with them.

The 39 inlets included in this study are listed in Table I together with 5 whose oceanography has not yet been studied. All but 3 of the inlets are in the mainland coast proper; these three, Surf, Laredo and Pendrell, are in islands but are so closely associated with the mainland coast that they have been included in the present study.

When referring to position along the inlets, the term "head" is applied to the inland end and the term "mouth" to the seaward end. In several cases, the complicated topography makes it difficult to determine the mouth precisely, and the selection of its location from a chart alone may be rather arbitrary.

The chief observations made during the cruises were of depth, salinity, temperature, oxygen content, and turbidity of the water, plankton distribution, and bottom material.

TABLE I. Salient dimensions of British Columbia mainland inlets.

Name	Abbrevia- tion	Length	Mean width	Mean mid- inlet depth	Maximum depth	Outer sill depth (Note 1)	Notes
		<i>nautical miles</i>		<i>m</i>	<i>m</i>	<i>m</i>	
Portland Canal	PoC	62	1.2	255	385	98	2
Portland Inlet	Pol	24	2.9	400	715	183	2
Observatory Inlet	Ob	41	1.2	385	530	46	3
Alice Arm	AA	10	0.7	240	385	18	2
Khutzeymateen Inlet	Kh	20	0.6	110	150	55	2,4
Work Channel	Wo	29	1.1	240	330	21	3
Porcher Inlet	Por	10	0.6	75	190	6	2,4
Douglas Channel	Do	45	1.9	330	455	210	2
Kildala Arm	Ki	10	0.8	175	240	162	2
Gardner Canal	Ga	70	1.0	275	500	37	2,5
Surf Inlet	Su	12	0.5	220	330	107	2
Laredo Inlet	La	21	0.8	295	400	128	2
Mussel Inlet	SM	18	0.8	275	435	146	3,6
Kynoch Inlet	MK	30	1.1	435	640	330	3,7
Spiller Channel	Sp	25	1.0	255	455	183	3
Briggs Inlet	Br	10	0.5	...	...	...	8
Roscoe Inlet	Ro	23	0.6	135	240	128	3
Cascade Inlet	Cas	14	0.6	250	305	128	3
Dean Channel	De	60	1.3	420	550	275	2,3
Kwatna Inlet	Kw	13	1.1	345	580	400	3
Burke Channel	Bur	56	1.4	400	550	43	3,9
South Bentinck Arm	SB	20	1.2	240	455	73	3
Rivers Inlet	Ri	25	1.6	295	365	137	2
Moses Inlet	Mo	14	0.5	200	290	37	2
Draney Inlet	Dr	13	0.5	90	145	11	3
Smith Inlet	Sm	18	0.7	270	365	122	2,3
Alison Sound	Al	11	0.5	...	185	...	4,10,11
Mereworth Sound	Me	10	0.5	...	185	...	4,10,11
Belize Inlet	Be	28	0.6	255	400	18	3,11
Nugent Sound	Nu	13	0.4	75	150	18	4,11
Seymour Inlet	Se	36	0.9	420	620	18	3,11
Drury Inlet	Dru	12	0.7	...	100	17	2
Kingcome Inlet	Kin	36	1.3	335	483	128	2
Knight Inlet	Kn	70	1.6	295	540	64	2
Call Inlet	Ca	15	0.8	135	209	48	2
Loughborough Inlet	Lo	19	0.9	190	260	128	2
Bute Inlet	Bu	41	2.0	510	660	355	2,12
Toba Inlet	To	20	1.4	390	505	490	2,12
Pendrell Sound	Pe	6	0.7	200	440	200	3
Jervis Inlet	Je	48	1.7	495	730	385	2
Princess Louisa Inlet	PL	4	0.4	120	180	6	2
Sechelt Inlet	Sec	22	0.8	190	300	14	2
Howe Sound	Ho	23	3.8	225	325	70	2
Indian Arm	Ind	14	0.7	130	218	20	2

NOTES:

(1) Depths are given for lowest normal tides. The tidal range varies from about 4 m at the south (Indian Arm) to 7 m at the north (Portland Inlet) and therefore the depth of water over the sills will periodically be increased by 4 to 7 m.

(2) Soundings from Canadian Hydrographic Service charts or field sheets (Portland Inlet and Canal from Admiralty Charts).

(3) Soundings during oceanographic cruises of Institute of Oceanography, University of British Columbia.

(4) Not yet visited by University of British Columbia.

(5) Sill depth quoted for exit through Ursula Passage, but Gardner also connects to Douglas through Devastation Channel, minimum depth 103 m.

(See additional notes at foot of opposite page.)

The depth measurements were made because before 1951 the majority of the inlets visited had either not been sounded or only partly sounded principally for navigation purposes. From echo sounder records and wire soundings, longitudinal profiles were prepared, but this part of the work was only incidental to the remainder of the program.

The main program consisted in the occupation of oceanographic stations at approximately 5-mile (9-km) intervals along the centre lines of the inlets, the locations being chosen as far as possible on straight sections rather than at bends. At each station serial observations were made of temperature, salinity and oxygen content of the water at as many as thirteen depths between the surface and close to the bottom. In each inlet and at each station the sampling depths were selected to permit the drawing of the salinity-depth curve with the minimum of individual interpolation. The necessity to adjust the depths arose chiefly in the surface layers (to about 30 m) because the main change in salinity takes place within this range. Temperatures were measured both with Richter and Wiese reversing thermometers, mounted on Atlas, Ekman or Fjarlie water sampling bottles, and with bathythermographs. Supplementary bathythermograph casts were frequently taken between the oceanographic stations.

The salinity was determined by titration of 10-ml samples by the Mohr method while the oxygen content was determined by the Winkler method using 250-ml samples.

At each station a Secchi-disc reading was taken together with observations of wind, air temperature, cloud cover and sea state.

Samples of the bottom sediments were obtained at some stations with either (a) a LaFond-Dietz bottom snapper (LaFond and Dietz, 1948) for the surface layers or (b) an Emery-Dietz-type gravity corer (Emery and Dietz, 1941) using a 3-foot by 1½-inch (1-m by 3.7-cm) core tube with lead weights to give a total weight of 70 lb (32 kg).

Some observations were made of internal waves with a direct-reading electrical resistance thermometer using a thermistor bead as temperature-sensitive element on a 25-m cable. For observations at greater depths a series of bathythermograph casts was used.

A vertical plankton haul and horizontal tows at four depths were made with Clarke-Bumpus samplers at alternate stations. The plankton distribution has been described by LeBrasseur (1954, 1955).

TABLE I.—NOTES—*Continued*

- (6) From mouth of Sheep Inlet to head of Mussel Inlet.
- (7) From west end of Oscar Passage, up Mathieson Channel to head of Kynoch Inlet.
- (8) Not sounded; maximum of a few soundings in Briggs Inlet in 1956 was 70 m.
- (9) Sill depth quoted for junction with Fitzhugh Sound, but Burke also connects with Dean through Labouchere Channel which is at least 400 m deep. (Ref. Note 2 above.)
- (10) Not sounded in detail.
- (11) Thompson and Barkey, 1938.
- (12) But both Bute and Toba communicate with the Strait of Georgia through Sutil Channel which has a sill of depth 252 m.

Bute was the first inlet visited in 1951. Two weeks were spent in occupying each station a number of times to gain some familiarity with the distribution of characteristics and the effects of the tide in order to assist in planning the remainder of the 1951 study. In the other inlets the stations were occupied during a single visit to the inlet. In some cases the stations were occupied once only; in other cases it was possible to occupy stations both while proceeding to the head of the inlet and also on the return. During subsequent cruises many of the stations were reoccupied and a number of anchor stations were occupied for periods of several days.

2. GENERAL CHARACTERISTICS

2.1 INLET DEPTH PROFILES

Of the inlets in the mainland coast, twelve had been surveyed and detailed charts published by the Canadian Hydrographic Service before 1950, and since that time charts have been published for four others. The majority of the remainder have been surveyed by 1960. For those for which Canadian charts are not published it is necessary to rely upon the older Admiralty charts in which the shoreline is delineated reasonably well but in which depths are given only in isolated shallow localities. As the bottom profile is an inlet characteristic which may have a considerable influence on the water circulation, the echo sounder records were retained from cruises in those inlets not previously surveyed. From these, and from wire soundings obtained when bottom sampling, longitudinal depth profiles were prepared. The physical features of the inlets obtained from these data have been described previously (Pickard, 1956) but as some of the characteristics are relevant to the present discussion they are summarized here. The dimensions at sea level, and the average and maximum depths for the inlets obtained from the published charts or from cruise soundings are included in Table I. Longitudinal profiles are shown in Fig. 3, 4, and 5.

The general form of the southern inlets from Howe to Toba has been described by Carter (1934) and his description is applicable to most of the mainland inlets. They are generally deep, and narrow in relation to their length. The origin of the inlets has been discussed (e.g. Bancroft, 1913; Carter, 1934; Peacock, 1935) and it appears that both structural changes and glacial action contributed to their formation. The bottom profiles of the inlets generally show considerable variations in depth from head to mouth, the chief exceptions being Toba, Bute, Knight, Kingcome, Rivers and Douglas. The detailed Canadian Hydrographic Service surveys of Jervis, Bute, Kingcome, Douglas and Gardner show that there are considerable stretches of flat and often level mud bottom in these inlets. The significance of this is commented upon later.

Very shallow entrance sills, such as those in some Norwegian fjords (Strøm, 1936) where the sill depth is less than the depth of the brackish surface layer,

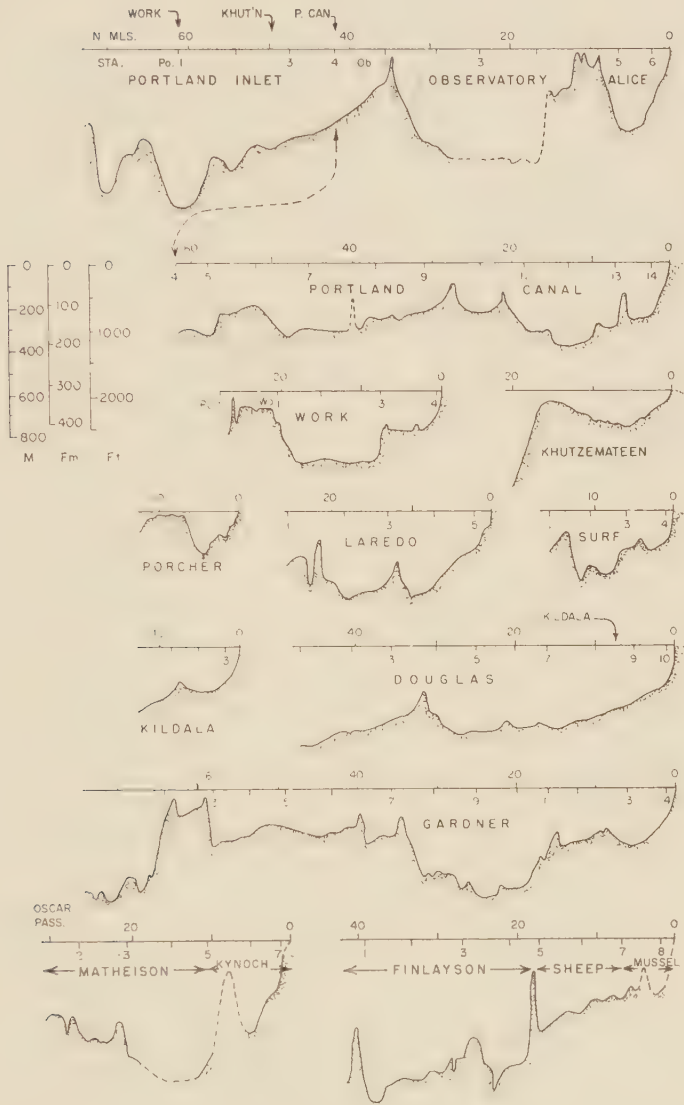


FIG. 3. Longitudinal sections along British Columbia mainland inlets, northern group.

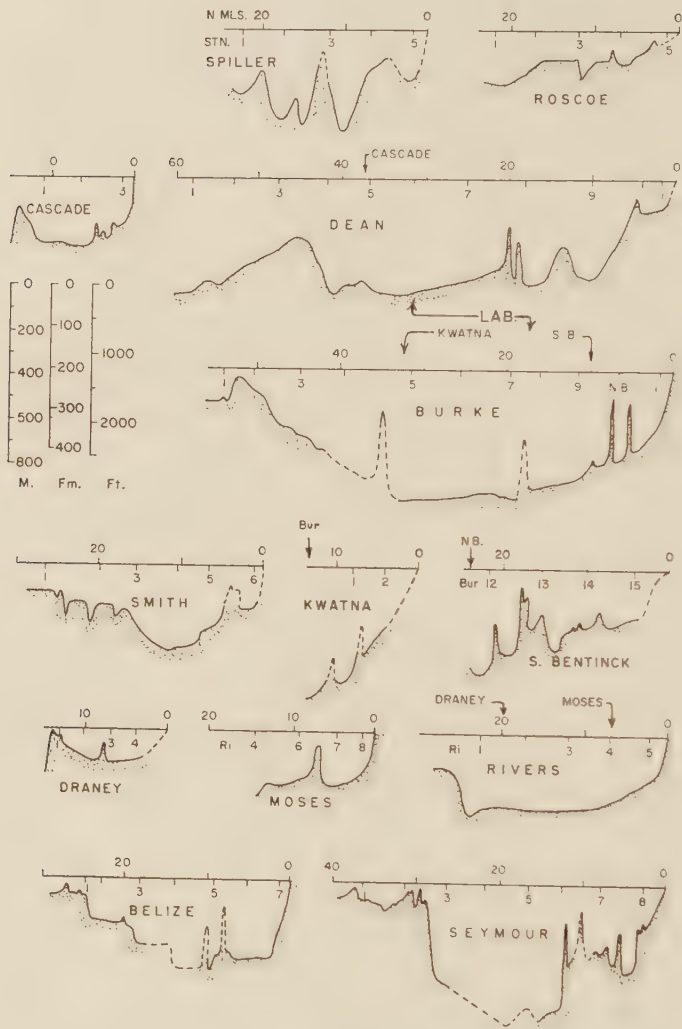


FIG. 4. Longitudinal sections along British Columbia mainland inlets, middle coast group.

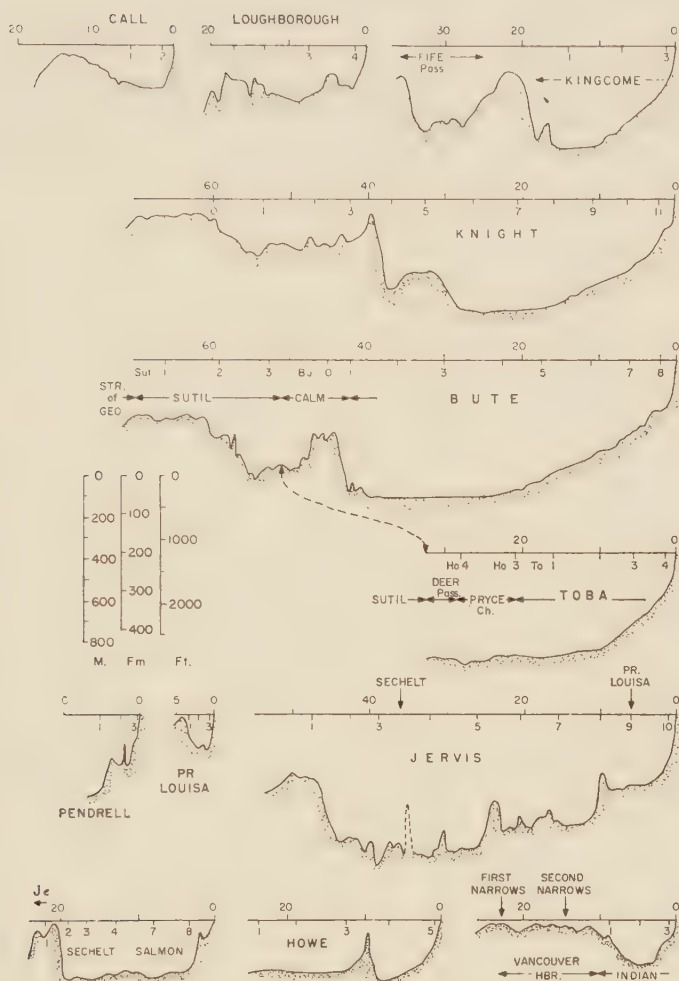


FIG. 5. Longitudinal sections along British Columbia mainland inlets, southern group.

are not found at all. A few inlets, as indicated in Table I, have sills of moderate depth (6 to 21 m) but in most cases the sills are deep. At the same time it must be remembered that the coastal seas into which all the inlets open are appreciably shallower (110 to 170 m) than the average in the inlets themselves. This feature is said to be typical of fjord coasts (Dinse, 1894).

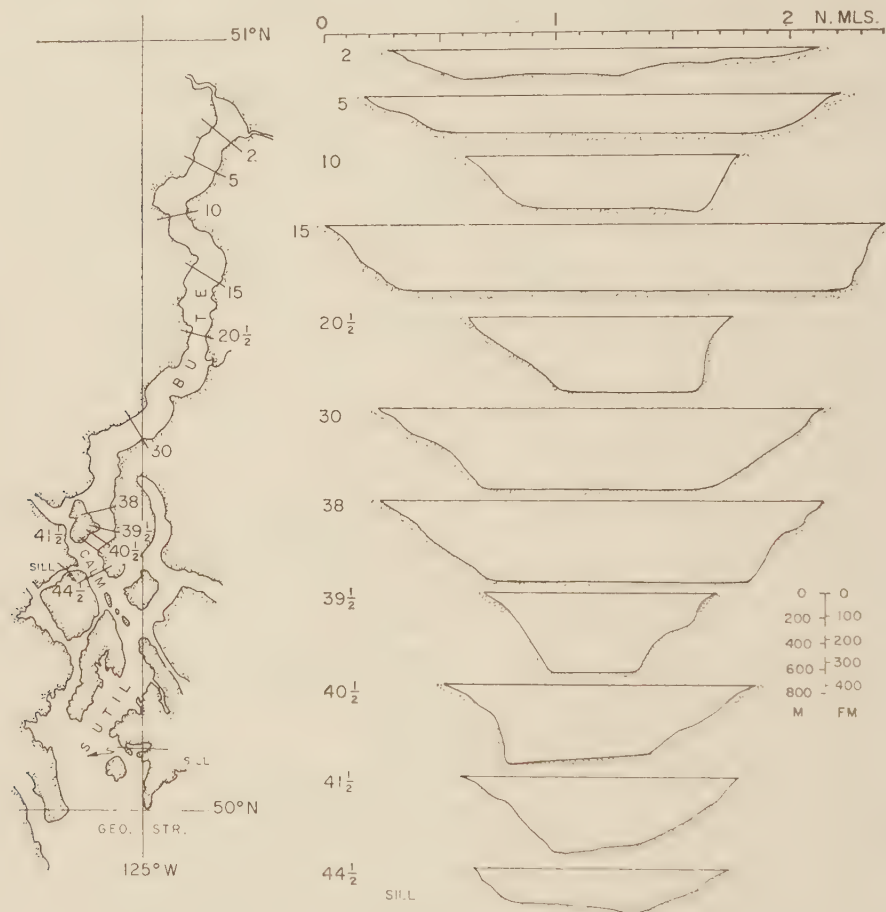


FIG. 6. Bute Inlet: transverse sections with same scale vertical and horizontal.

Figure 6 shows a selection of transverse sections across Bute drawn with no vertical-to-horizontal scale exaggeration. The distinctive features of these sections are the steep sides and the flat floor for the greater part of the inlet length. This flat floor appears to be characteristic of many of the large inlets into which considerable rivers flow. The superficial sediments are glacial silts (Toombs, 1956) and it is presumed that the flat floor is the result of a uniform settlement of this material from the water, the sediment being carried along the inlet either in the outflowing surface layer or by the agency of turbidity currents.

The relatively small amount of sediment found in the surface water layer suggests that the turbidity currents are probably the chief agent.

Figure 7 shows a selection of sections across Jervis, again with undistorted scale. The most notable difference from Bute is the absence of a flat bottom to seaward of section 7. The river inflow to Jervis is smaller than into Bute and there is a smaller concentration of suspended material in it. Presumably the material brought in at the head is trapped by the inner sill at about section 10. However, the fact that it reaches to this sill, and in fact is most conspicuous just inside the sill where the inlet is deeper than near the head, is regarded as significant. It again suggests that mud slides may take place from the inlet

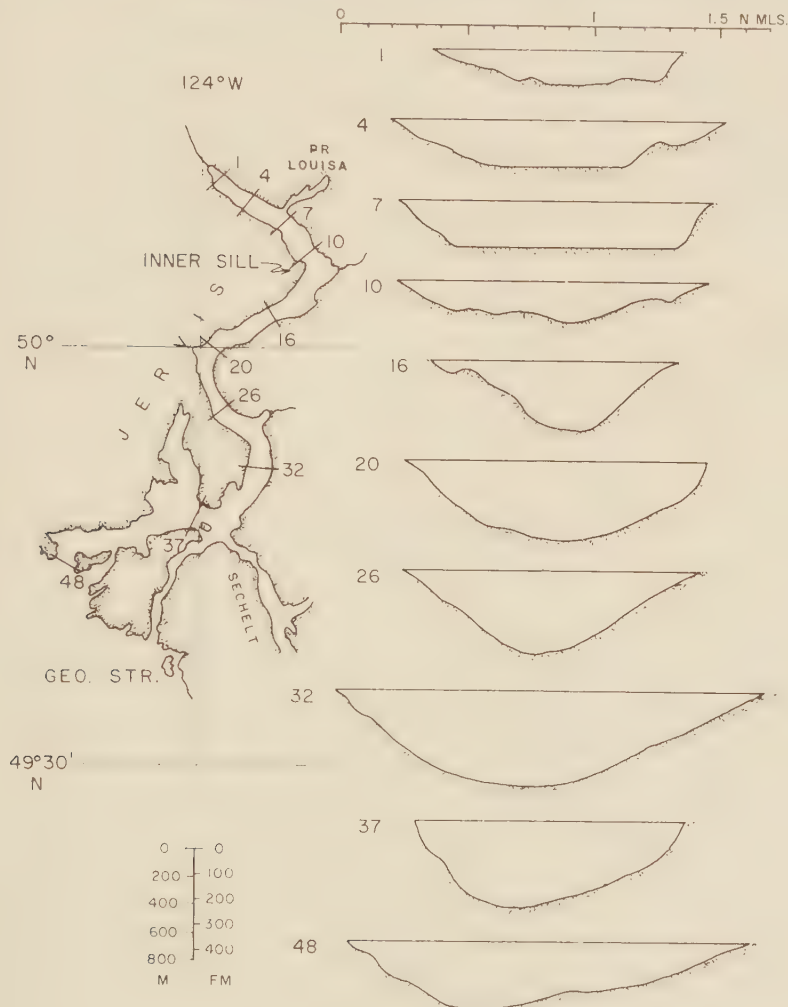


FIG. 7. Jervis Inlet: transverse sections with same scale vertical and horizontal.

head and cause turbidity currents which carry material along the bottom to the deepest part of the basin inside the sill. This hypothesis is supported by the evidence from Bute and Kingcome which have no inner sill and in which the very flat section is inside the outer sill and some 30 and 15 miles (56 and 28 km) respectively from the head. Further evidence for the frequent occurrence of turbidity currents has been put forward as a result of studies of optical turbidity due to particulate material in the inlet waters (Pickard and Giovando, 1960).

In Gardner (not illustrated), flat bottom sections are found to seaward of rivers entering at the head and at the side. This suggests that they are the result of direct deposition of river-transported material. A conspicuous flat section is found just to seaward of the Kemano River, but in this case it is not terminated at a sill. A deeper section with irregular bottom topography in transverse section is found only 3 miles beyond the flat one.

The profiles in Fig. 6 and 7 are drawn with no vertical-to-horizontal scale exaggeration and show that in many cases it will probably be possible, for theoretical study, to approximate the cross-section by a simple rectangular or trapezoidal form without significant error.

In plan form, on the other hand, the charts show that very few of the inlets are regular in shape. Sharp bends of 90° or more and variations in width by a factor of 2 are common (e.g. Fig. 1, 2, 6, 7). Observations of currents during cruises in 1952, 1953 and 1955 indicate that both the tortuous form of the inlets and the bottom irregularities where they occur have a profound influence on the local character of the flow. These irregularities in form are factors which have in the main been largely ignored in theoretical studies but which make it difficult to obtain representative current measurements for comparison with theory.

2.2 BOTTOM MATERIALS

The character of samples of the bottom materials obtained with a snapper or a small gravity corer at 5- or 10-mile intervals has been described briefly (Pickard, 1956). The material was predominantly fine-grained mud, with sand in some samples, and occasionally pebbles or shells. About 75% of the mud samples were light to dark grey in colour when wet (from inlets with large run-off) and the remainder were greenish brown (from low-runoff inlets). Only a small percentage of samples smelled of H_2S . These were in the green-brown colour group, the grey samples having no smell.

The samples obtained in 1951 and 1952 in Bute were examined and described by Toombs (1956). He reported that the predominant minerals were quartz, feldspar, and biotite, while the organic content was very low (1 to 4%). No detailed study has been made of samples from other inlets but from field examination it is believed that the Bute results may be regarded as typical for the inlets with glacial runoff. It is probable that the bottom sediments in the small-runoff inlets have a higher organic content than those in Bute.

2.3 FRESH WATER DISCHARGE INTO THE INLETS

Since the inlets are estuarine in character, information on the fresh water discharge into them is important but is unfortunately very scanty. However,

Trites (1955) has combined what data are available for river flow with data on precipitation for the watersheds concerned and has estimated the fresh water runoff into many of the inlets. Some idea of the amount of runoff and of the variation between inlets is given in Table II in which are presented Trites' values for the mean annual discharge.

TABLE II. Mean annual discharge of fresh water into some British Columbia inlets (after Trites, 1955).

Inlet	Group ¹	Fresh water discharge <i>m³/sec</i>
Portland Canal	A.1	260
Portland Inlet (Nass River)	A.1	990
Observatory	A.1	160
Gardner	A.1	580
Dean (above Labouchere)	A.1	280
Dean (total)	A.1	730
Burke	A.1	420
Rivers	A.1	540
Draney	A.2	40
Smith	A.2	120
Belize	A.2	80
Seymour	A.2	100
Knight	A.1	410
Loughborough	A.2	100
Bute	A.1	410
Toba	A.1	270
Jervis (above Sechelt)	A.2	180
Sechelt	A.2	110
Howe	A.1	460

¹The significance of the grouping is explained in the text together with Table III and Fig. 4.

A method for estimating the fresh water transport along an inlet from the heat budget has been described and examples of its application are given by Pickard and Trites (1957). This offers a means for estimating the fresh water runoff into an inlet from observations of the distribution of temperature and salinity in the upper layers along the length of the inlet.

A pronounced seasonal variation in runoff occurs and the character of this is shown in Fig. 8. The majority of the inlets, including all the longer ones except Jervis and Observatory, have a considerable discharge, most of which comes from the summer melting of precipitation occurring during the winter as snow on higher inland elevations. The runoff to the majority group of inlets is a minimum during January–March and a maximum during May–July, with a secondary maximum in October. These inlets are combined as Group A.1 in Fig. 8, and examples of the annual variation are given for two southern inlets, (Bute and Knight) and for a northern inlet (Portland). The remainder of this group

fall between these limits. The lower minimum and higher maximum for Portland as compared to Bute are presumably due to climatic difference.

The minority of the inlets, mostly short ones, are not fed from stored runoff and show a different annual cycle as in Group A.2 in Fig. 8. Among this group the runoff is above average in the spring and in the winter months and below average during July–September, following the coastal rainfall pattern closely. The effect of this variation of runoff pattern on the surface layer of the coastal waters has been described by Pickard and McLeod (1953).

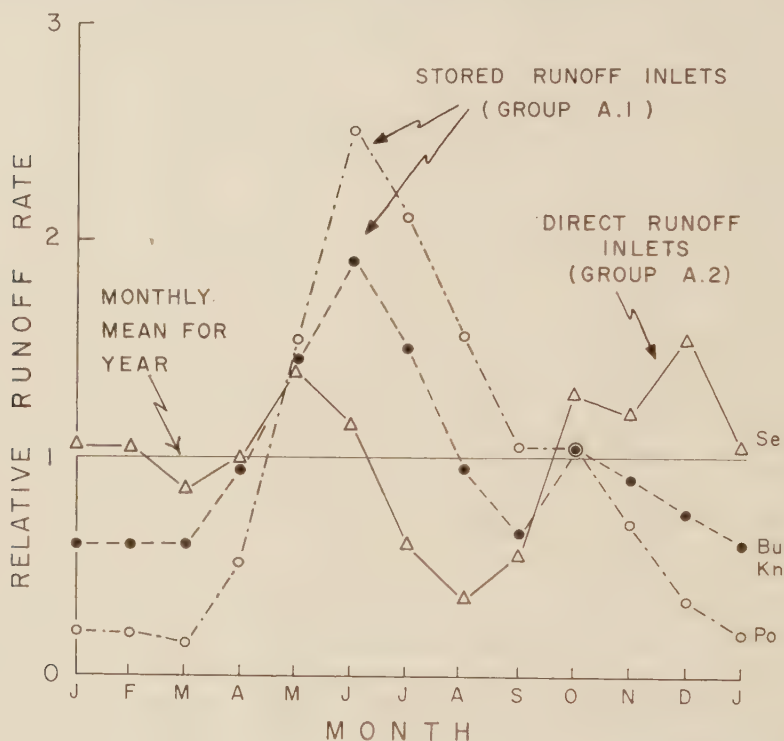


FIG. 8. Monthly runoff typical of stored runoff (Group A.1) and of direct runoff (Group A.2) inlets expressed as multiple of monthly mean for whole year.

2.4 TIDES

The principal characteristics of the tides of the British Columbia coast are that they are semi-diurnal and markedly declinational (having a marked inequality between the heights of successive low waters), and that the range increases from south to north. In the south at Point Atkinson near Vancouver the maximum range between low and high waters of large tides is 4.8 m, while at Prince Rupert in the north it is 7.6 m and at Stewart at the head of Portland Canal it is 8.0 m. Between the mouth and head of each inlet there is little difference in tide. At the head the time of high or low water is later by not more than 10

minutes than at the mouth, while the range is only from 1 to 10% greater than at the mouth (Dawson, 1920; Canadian Hydrographic Service, 1960).

2.5 NON-TIDAL OR ESTUARINE CIRCULATION

In his journal (1798, Vol. I, p. 309) Vancouver remarks: "In all these arms of the sea we had constantly observed, even to their utmost extremity, a visible, and sometimes a material rise and fall of the tide, without experiencing any other current than a constant drain down to the seaward, excepting just in the neighbourhood of the gulf." This net seaward motion is now recognized as a consequence of the discharge of fresh water into the heads of the inlets. The low-salinity surface layer so formed flows seaward, gaining in volume by entrainment of saline water from below as it does so and gaining in speed as it approaches the inlet mouth. The resulting unidirectional flow is superimposed on the flood and ebb due to the tide to decrease the speed of the former and increase that of the latter. It may even prevail over the flood to the extent of preventing any inward flow, the resultant being a seaward flow at all times but fluctuating in speed with tidal period. A further consequence of the entrainment of saline water into the outflowing surface layer is a subsurface inflow. The whole pattern of surface outflow and subsurface inflow is referred to as an "estuarine circulation". It has been described in detail for Alberni Inlet by Tully (1949), the dynamics have been discussed theoretically by Cameron (1951), and Pritchard (1952) has brought together the results of these and other workers with his own studies. Pickard and Rodgers (1959) have described more recent direct measurements of current in Knight. These suggest that the water movements in a deep inlet may be more complex than previous theoretical studies have assumed but support the net circulation pattern described above. Therefore in the present paper the estuarine circulation will be considered an established and expected feature of the British Columbia inlets.

3. SALINITY AND TEMPERATURE

The waters of all the inlets show marked horizontal stratification of both salinity and temperature, particularly near the surface. The water becomes more saline and, with some exceptions to be discussed later, colder with increase in depth. The salinity stratification is a consequence of the inflow of fresh water from the rivers, while the temperature stratification is a consequence of solar heating combined with the marked stability of the surface waters due to the salinity structure.

In describing the salinity and temperature distributions it is convenient to divide the water into two main depth zones, shallow and deep. The water in the first is fresh or brackish, while in the second it approximates in salinity to the water of the coastal seas. When considering the dynamics of the flow and the process of mixing between the fresh and salt waters it is necessary to subdivide the shallow zone into a surface zone and an intermediate or mixing zone (Tully, 1949). The depths of the surface and mixing zones vary from inlet to inlet, and

from time to time, and may be considered oceanographic characteristics of these bodies of water.

The inlets can be divided broadly into two groups:

- A. those with a low surface salinity at the head, and
- B. those with a relatively high surface salinity at the head.

Group A can be subdivided into possibly two subgroups (A.1 and A.2) in terms of salinity at the head and mouth. This division is shown in Table III,

TABLE III. Surface salinities, Secchi-disc readings and types of salinity profile in British Columbia inlets¹.

Group A.1				Group A.2			Group B				
Surface salinity											
Head 0.1– 2‰				1–11‰			18–29‰				
Mouth 5 –20‰				15–29‰			20–31‰				
Secchi-disc depth											
Head 0.3–1 m				4–7 m			6–10 m				
Mouth 2 –8 m				3–7 m			4–11 m				
Salinity profile type ^a											
	Mo	Mi	Hd ^b		Mo	Mi	Hd		Mo	Mi	Hd
Portland C.	1a	1b	1a	Sheep	2	2	2	Work	1c	1c	2
Observatory	1b	1b	1b	Spiller	2	1c	1b	Surf	2	2	2
Kildala	1b	1b	2	Roscoe	2	2	2	Laredo	2	2	2
Douglas ⁴	1c	1b	1b	Draney	2	2	1b	Kynoch	1c	1c	2
Gardner	2	1b	1a	Smith	2	2	1b	Briggs	2	2	...
Cascade	1b	1b	2	Belize	1a	1b	2	Drury	2	2	...
Dean	1b	1b	1a	Seymour	2	2	2	Call	1c	...	1c
Burke	2	1b	1a	Loughborough	2	1b	1b	Pendrell	1c	...	1c
Rivers ⁴	2	2	1a	Jervis	1c	2	2		or		or
Kingcome	1b	1b	1a	Sechelt	2	2	1b		2	...	2
Knight	1b	1b	1a	Indian	1b	1b	1b				
Bute	1c	1b	1a								
Toba	1c	1b	1a								
Howe	1b	1b	1a								

¹A number of the smaller inlets, particularly those which are side arms of larger inlets, are special cases and have been omitted from this tabulation.

²The types of salinity profile are indicated in Fig. 15 and described in the text.

³Mo = mouth; Mi = middle; Hd = head of inlet.

⁴At head, surface salinity = 1 to 3‰, Secchi-disc depth = 1 to 2 m.

together with some data on salinity–depth profiles and on Secchi-disc depths which it is convenient to associate with the salinity data for subsequent discussion of the significance of the division. Group A.1 includes the inlets with the larger runoffs, in most cases from glaciers or snowfields, and Fig. 9 shows vertical profiles of temperature, salinity and oxygen for a typical example (Bute). Group A.2 includes inlets with medium runoff with little or no contribution from glaciers, etc. Figure 10 shows profiles of the water characteristics for Seymour as an example.

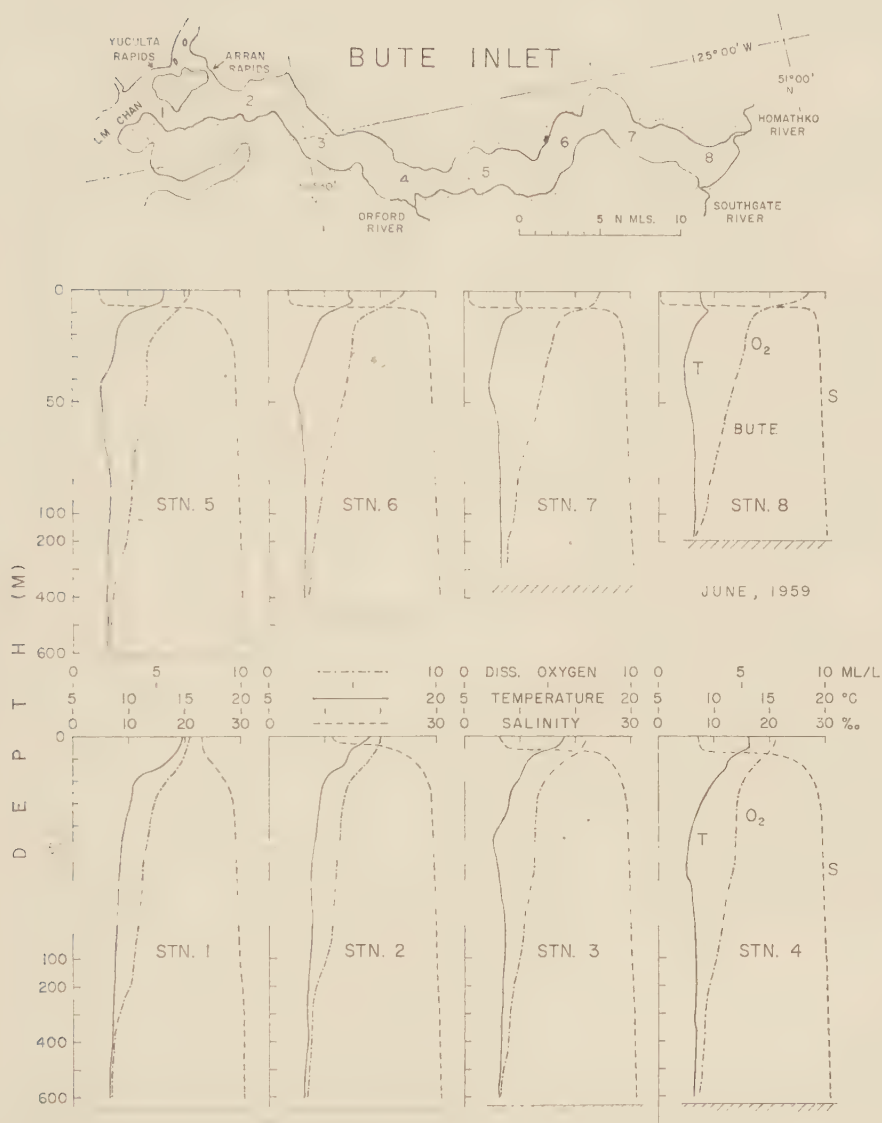


FIG. 9. Vertical profiles of salinity, temperature and dissolved oxygen in a large-runoff inlet (Bute).

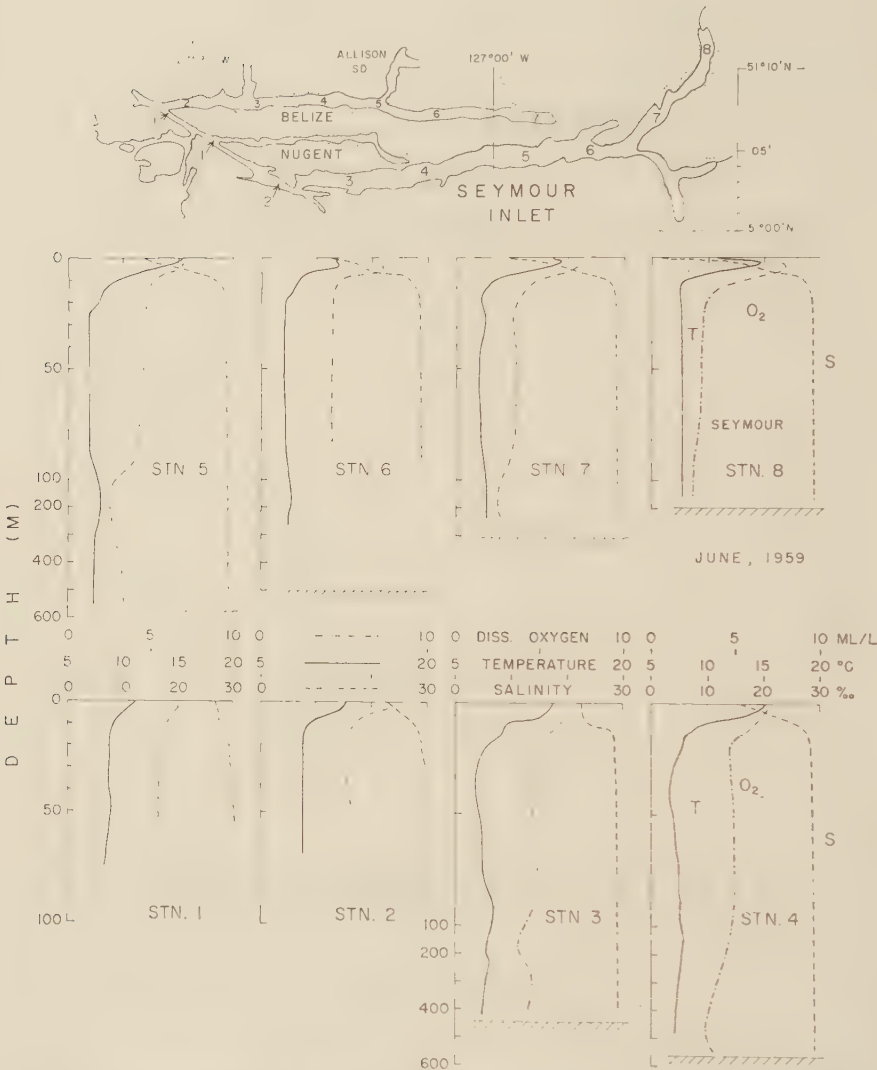


FIG. 10. Vertical profiles of salinity, temperature and dissolved oxygen in a medium-runoff inlet (Seymour).

Group B is a small one including the inlets with small runoff and consequently higher surface salinities, particularly near the head. Figure 11 shows profiles of water characteristics for Laredo as an example.

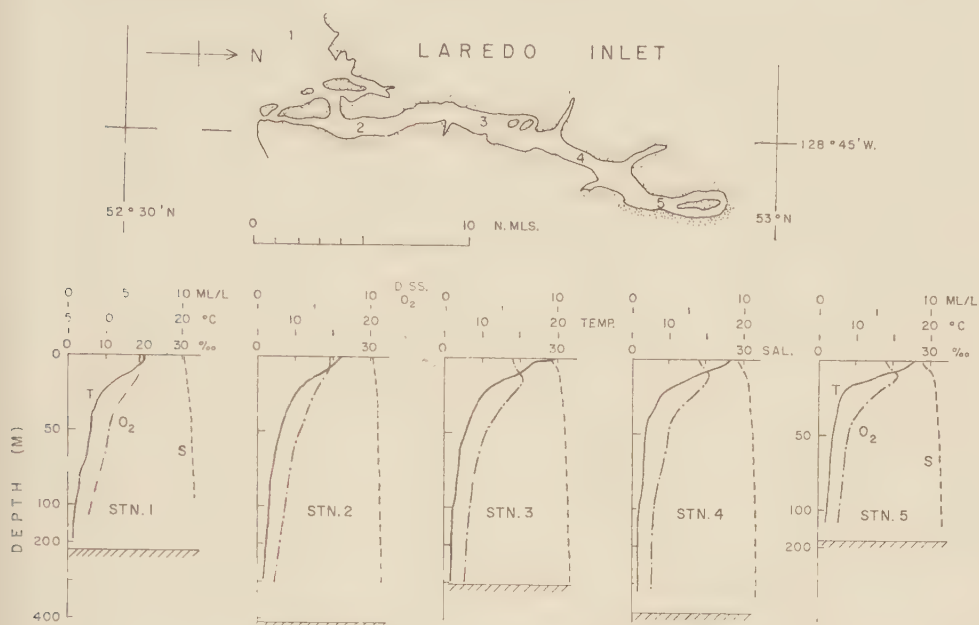


FIG. 11. Vertical profiles of salinity, temperature and dissolved oxygen in a small-runoff inlet (Laredo).

In the majority of cases the salinity of the water at a depth of 20 m in an inlet is at least 90% of that of the deepest water in the particular inlet. Since it is convenient to describe the shallow and the deep zones separately this depth of 20 m is arbitrarily taken to divide the two zones in the following description of the main characteristics. The actual depth of the halocline in the different inlets will be discussed in a subsequent section.

3.1 SHALLOW ZONE

The major characteristics of the shallow zone are the general presence of (1) variations of both salinity and temperature along the length of an inlet, and (2) variations in vertical profiles of salinity and temperature along individual inlets and between inlets.

3.11 SALINITY DISTRIBUTION AT THE SURFACE

The surface sample was drawn either from a bucket sample or from a reversing water bottle with its upper end just beneath the surface. It is taken as characteristic of the top $\frac{1}{2}$ -m layer of water.

The general character of the distribution of surface salinity (and temperature) along the inlets is shown in Fig. 12-14. Figure 12 shows a selection of longitudinal profiles for a Group A.1 inlet, Bute, and its continuation along Calm and Sutil Channels to the Strait of Georgia. The profiles are for different months and show that a marked seasonal variation occurs. The first profile, for February, is typical of the winter, when the river runoff is least. The salinity is then almost uniform

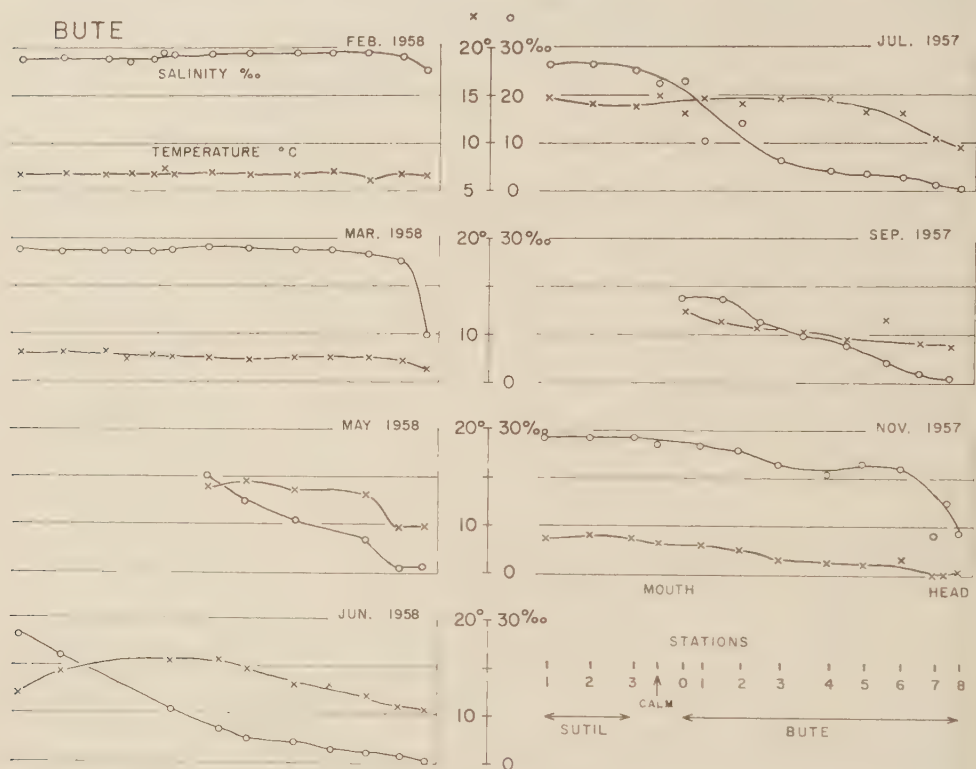


FIG. 12. Longitudinal profiles of salinity and temperature at the surface in a large-runoff inlet (Bute) showing seasonal variation.

along the inlet and channels and has its highest value for the year. The March profile shows a fall in salinity at the head as the river runoff starts to increase, probably chiefly from snow melt at lower elevations at this time. By May the salinity along the greater part of the inlet length has fallen below 20‰, and by June below 10‰. The abrupt change between Sta. 7 and 6 in the May profile is characteristic for a brief period at that time of the year. It is evidence of a low-salinity front which is a consequence of the rapid rise in runoff in the spring. The low-salinity water is silty and it can be seen to advance down the inlet in a period of a few days to change the surface salinity quickly from the high values of the winter regime to the low values typical of the summer as shown for June. The July profile shows low salinities still in the inner half of the inlet itself but a rise to Strait of Georgia surface values near the mouth (about Sta. 1) and along the

channels. This is because the runoff generally decreases in July and is insufficient to maintain low values in the outer passages (Calm and Sutil). The September and November profiles show a progressive return to the winter regime of high surface salinity.

Figure 13 shows some summer profiles for Knight, another Group A.1 inlet, having longitudinal distributions similar to those of Bute. No winter data are available for Knight. The same Figure also shows summer and winter profiles for Jervis which has a smaller runoff than Bute and is in Group A.2. The winter condition, of which the November profile is typical, is again one of uniform salinity along the inlet. The earlier decrease in salinity in Jervis (February) compared to Bute (March) may be due to differences in the pattern of precipitation or direct runoff which is the main source of fresh water in Jervis. The minimum salinity values are observed during June–July, the values not being as low as in Bute. Note that in Fig. 13 and 14 all the inlets have been scaled to the same length for convenience in comparison.

Figure 14 shows, on the left, summer profiles for some of the inlets further north. Portland, Gardner and Dean in Group A.1 show profiles similar to Bute and Knight. The longitudinal profile for Douglas, which is classed as a Group A.1 inlet in Table III on the basis of vertical profiles, is more like that for Jervis in Group A.2. The rapid rise in salinity midway along Burke, which has a large runoff from the Bella Coola River, may be the result of some of this surface low-salinity water moving to the right out of Burke through Labouchere Channel into Dean (see Fig. 1).

On the right in Fig. 14 are profiles for Smith and Seymour which are Group A.2 inlets (medium-runoff, non-glacial). Belize has only a very small runoff at the head, most of the fresh water appearing to enter at the north side from Alison Sound at the position corresponding to the dip in the salinity profile. Spiller might be expected to be one of the lower-runoff Group A.2 inlets, and the moderately low values of salinity at the head may be a consequence of the long restricted mid-section of the inlet limiting exchange with the outside. The profile for Surf is typical of the Group B very-low-runoff inlets with little longitudinal variation of salinity.

The distribution of surface salinity probably affords a better criterion of the location of the inlet mouth than does the mere geometry of the shorelines. For instance, it is clear that the influence of Bute runoff can be traced as far as Sutil Channel in summer and a synoptic survey to describe Bute should be continued out to this region. On the other hand, the salinity (and temperature) profiles for Jervis reach steady values within the inlet even in summer. (It must be pointed out that the values of salinity in the Strait of Georgia at the mouth of Jervis fall from about 28‰ in winter to 20‰ or less in summer (Waldichuk, 1957).) By this criterion, Dean in 1956 was not followed to its oceanographic mouth, which appears from 1951 data to be where Fitzhugh Sound opens into Queen Charlotte Sound.

The above comments all refer to observations taken along the approximate centreline of each inlet. A limited number of transverse sections across Bute have shown small salinity differences of up to 0.5‰ and temperature differences of

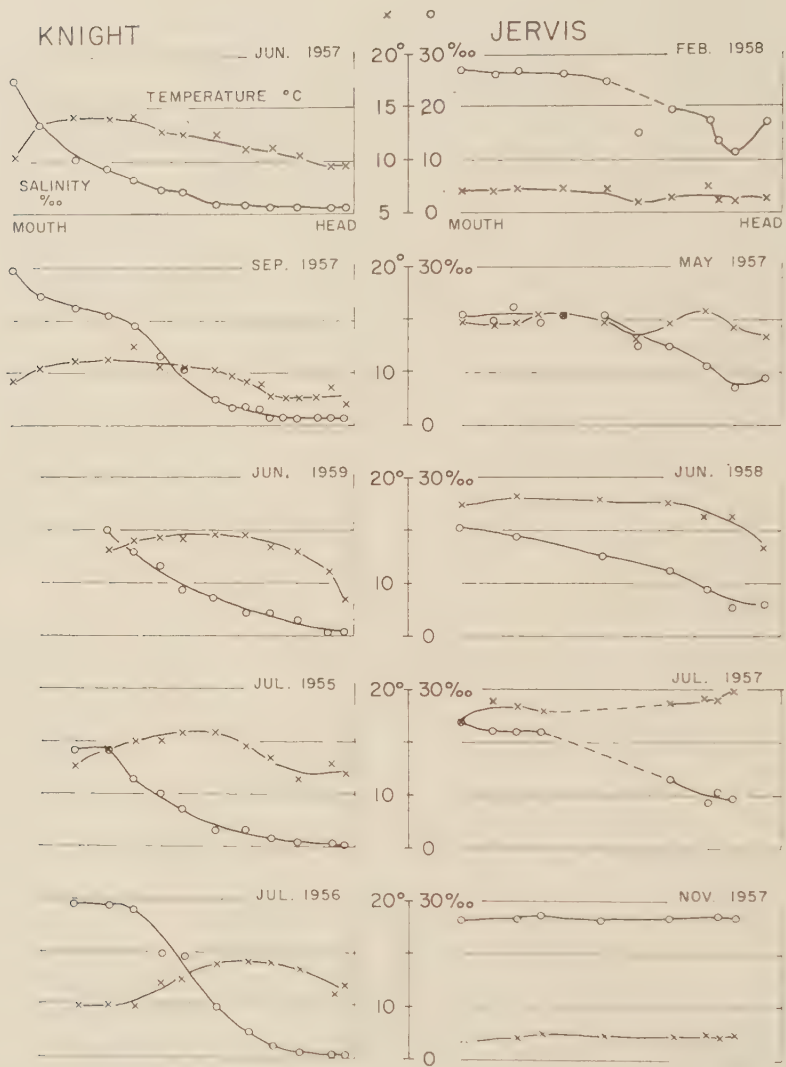


FIG. 13. Longitudinal profiles of salinity and temperature at the surface in large-runoff (Knight) and in medium-runoff (Jervis) inlets, showing seasonal variation in the latter.

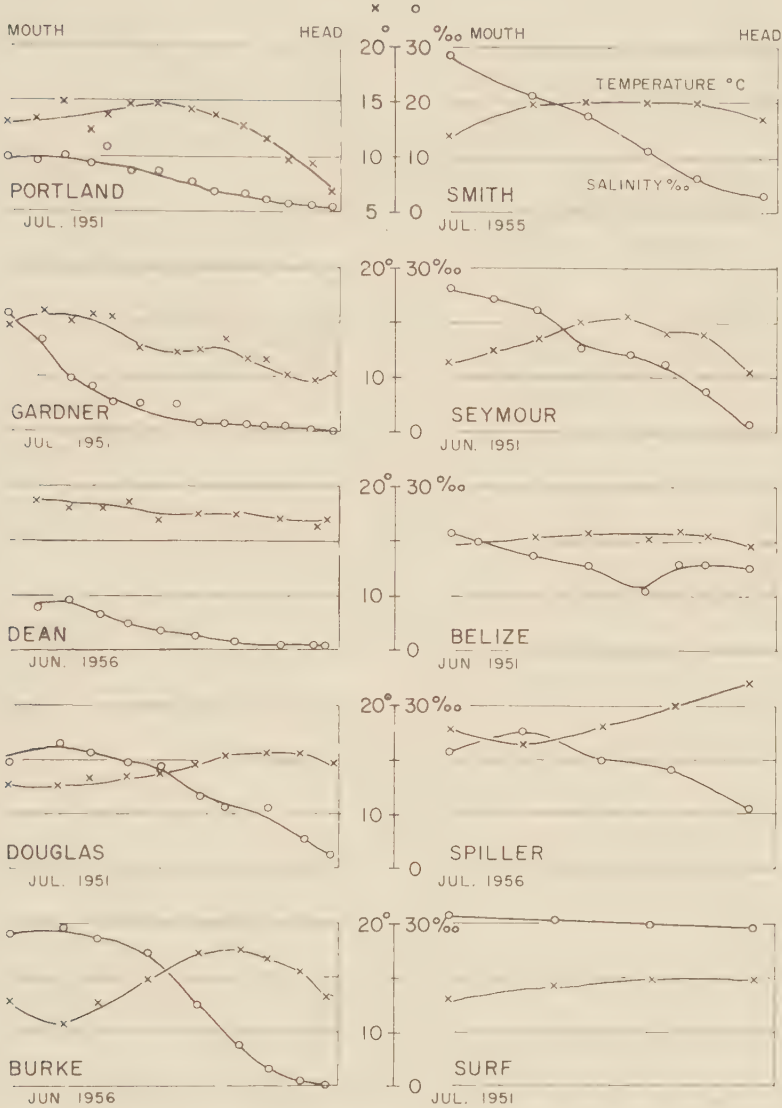


FIG. 14. Longitudinal profiles of salinity and temperature at the surface in large-, medium- and small-runoff inlets.

0.5 C degrees across the width of the inlet (Tabata and Pickard, 1957), the lower salinities and higher temperatures being on the west side (i.e. on the right when looking in the direction of net flow of the surface layer).

It is surprising that the group of inlets north of Ocean Falls, i.e. Roscoe, Spiller, Kynoch and Mussel, are in Groups A.2 or B since these inlets are in one of the regions of highest precipitation on the coast (over 150 inches (3.8 m) per year; Chapman and Turner, 1956). When visited in July 1956 these inlets had higher surface salinity values and lower total amounts of fresh water in the shallow zone than had most of the other large inlets. The probable explanations are that (a) these inlets have relatively small watersheds and therefore the large precipitation does not result in a large inflow of fresh water; (b) the runoff into these inlets probably occurs with only a short lag after the precipitation (the maximum values of precipitation occur in the winter but the only available oceanographic observations are from the summer period of small runoff); (c) there are only small glaciers or snowfields in the watersheds and therefore the stored runoff contribution to be expected in the summer is small.

Pendrell, although included in Group B, is unique among the inlets studied in that there is sometimes a salinity maximum at the head. The reason is that this inlet is located in a small island from which there is very little fresh water runoff. The salinity structure of the water in the body of the inlet is similar to that at the mouth of Toba and it is probable that the seasonal changes in salinity in Pendrell are the result of exchange of water with Toba via Homfray Channel. The surface temperature at the head of Pendrell in the summer is usually higher than elsewhere in this inlet or anywhere in the other southern inlets, and it is presumed that the salinity maximum here is the result of an excess of evaporation over precipitation plus runoff.

3.12 TEMPERATURE DISTRIBUTION AT THE SURFACE

Figures 12-14 also show typical temperature profiles for the surface water along the lengths of several inlets. Figure 12 shows profiles for Bute to demonstrate the seasonal variation from minimum values in winter to maximum values in summer, and to show the association between temperature and salinity profiles. The typical winter profile for February shows substantially uniform low temperatures along the inlet length and the channels connecting it to the Strait of Georgia. In May it is seen that with the rise in salinity between Sta. 7 and 6 there is a change in temperature. The low values at Sta. 8 and 7 to the right of the surface-water front emphasize the low temperature of the runoff water. In June, when a steady state has been reached, it is seen that the cold runoff water warms up as it moves along the inlet. It is this fact which was made the basis for the method for determining the fresh water runoff from heat budget considerations (Pickard and Trites, 1957).

It should also be noted that the temperature at the surface in June reaches a maximum at about Sta. 1, while in July the maximum is further up the inlet at Sta. 4. This longitudinal temperature maximum is characteristic of the large-runoff inlets, and other examples may be seen in Fig. 13 and 14. It is noted that this maximum occurs where the salinity starts to rise rapidly, and the

decrease to seaward is considered to be a consequence of increased upward mixing of cool, saline water from below. Examination of all longitudinal profiles available indicates that the temperature maximum along the Group A.1 inlets usually occurs where the surface salinity rises to between 6 and 10‰, usually at about 8‰. There is no obvious reason why 8‰ should be a magic value. It would be more reasonable to expect the increased vertical mixing to be determined by the stability of the water in the shallow zone rather than be associated with an absolute value of salinity, i.e. density. The possible significance of the association of the temperature maximum with the 8‰ isohaline remains to be investigated.

In Fig. 13, Knight again shows characteristics similar to Bute, with the exception that the temperature maximum occurs where the surface salinity is about 6‰. In Jervis, the higher temperatures at the head than in Bute are because the main runoff does not originate in glaciers and is of smaller volume.

In Fig. 14, Portland shows a low surface temperature at the head because much of the runoff comes only a short distance from glaciers and snowfields. The runoff into Gardner, Douglas, Burke and Dean, particularly the latter, travels considerable distances before reaching the inlets and is warmed by the sun and atmosphere more than are the rivers which flow into Bute and Knight.

The high temperatures at the head of Spiller are characteristic of the complex of inlets between Dean and Gardner. These inlets appear to have little stored runoff, and hence the speed of net outward flow in the summer in the surface layer is small and the water reaches relatively high temperatures in the inner reaches of the inlets. The highest temperature recorded in a mainland inlet in these studies was 24.3°C in Roscoe, one of this group. In Surf and Laredo the lower temperatures combined with high salinities must be due to the direct communication between the waters of these inlets and the waters of Hecate Strait which have similar temperature-salinity (T-S) characteristics.

3.13 SALINITY DISTRIBUTION WITH DEPTH IN THE SHALLOW ZONE

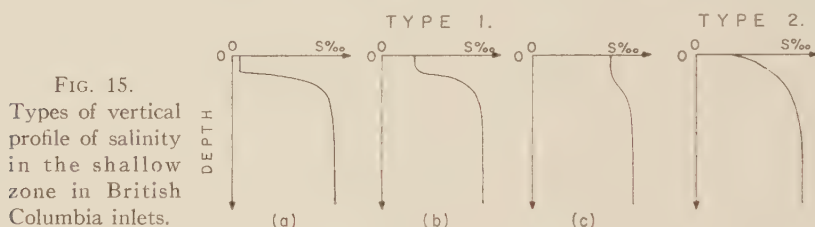
Immediately below the surface there is either a homogeneous layer or the salinity increases with depth. At the head of the inlets in Group A.1 there is a nearly homogeneous surface layer of low salinity whose lower limit is clearly defined at a depth of 3 to 10 m (e.g. Fig. 9, 16, 30). The depth depends upon the river inflow and the state of the tide. Below this depth the salinity increases rapidly to 25‰ or more at a depth of 5 to 12 m, the salinity gradient not uncommonly approaching 30‰ per metre in this halocline.

Near the mouths of the inlets of Group A.1 the salinity-depth profile shows a more gradual change from the surface salinity value to that in the deeper zone. Along the intervening length of the inlets a series of salinity-depth curves will show a steady transition from the two-layer system at the head to the more gradual change at the mouth. Figure 9 shows examples of such curves (cf. Tully, 1949, fig. 3, 4 and 5). Observations of the current distribution through the shallow layer have shown that there is often a marked velocity shear between the brackish surface water and the more saline water below it (Pickard and Rodgers, 1959). This shear is undoubtedly accompanied by turbulence which is chiefly responsible for the dilution of the originally fresh river water with salt water

entrained from below. The details of this process are at present imperfectly understood but are being studied.

The above remarks describe the variation of salinity with depth in broad terms. As this variation is the chief feature of these estuarial bodies of water it will be described in more detail.

The salinity-depth profiles are chiefly of one of two types. In Type 1 there is a more or less homogeneous surface layer and below it a distinct halocline, or region of large rate of change of salinity with depth, which separates the surface layer from the deeper zone of smaller rate of change. In Type 2 there is no homogeneous layer and the salinity increases with depth from the surface at a rate which decreases as the depth increases. Curves 1b and 2 in Fig. 15 show these basic types. In the case of Type 1 several variations occur. Type 1a,



in which the upper layer is nearly homogeneous, of low salinity, and with a clearly defined lower limit, is common at the heads of inlets with large runoff. A very large rate of increase of salinity with depth in the halocline is characteristic of these situations. Type 1c in which the surface layer is also homogeneous but of higher salinity is more common near the mouths of inlets, and the rate of increase of salinity with depth in the halocline is much less than in Type 1a. Occasionally the salinity-depth profile indicates the presence of more than one homogeneous layer in the surface zone.

The types of salinity-depth profile characteristics of the runoff period (May-August) are included in Table III. It will be seen that the distinct two-layer situation (Type 1a) is common in the inner parts of the inlets having low salinities (Group A.1 in Table III) because of the high runoff. Toward the mouth the curves change through Type 1b to Type 1c or 2 as mixing between the layers occurs. The inlets with low runoff generally have Type 2 curves even at the head. The Type 1c profile which is often seen at the mouth as a variant of the Type 2 is probably due to wind mixing of a previous Type 2 situation.

In comparing the shallow-zone salinity profiles of the various inlets a tabulation was made of the profile type and "dimensions". The latter include the surface salinity and a minimum of data necessary to indicate the location of the curve on a salinity-depth plot. The data used for this purpose were (a) the depth of the homogeneous zone (for Type 1 curves), (b) the depth at which the salinity reaches 50% of the deep water salinity (base salinity) for the inlet, (c) the depth at which the salinity reaches 90% of the base salinity. Table IV summarizes these values for the majority of the inlets.

The low-salinity homogeneous layer at the surface is characteristic of the inner part of an inlet. It is most sharply defined near the head and generally

TABLE IV. Dimensions of salinity-depth profile in shallow zone in British Columbia inlets.

	Depth of homogeneous layer near inlet head		50% depth			90% depth		Number of cruises
	Mean	Range	Mo	Mi	Hd	Mean	Range	
	<i>m</i>	<i>m</i>	<i>m</i>	<i>m</i>	<i>m</i>	<i>m</i>	<i>m</i>	
Portland C.	6	4.5-7.5	1.5	6.5	8	17	14-18	1
Observatory	8	6.5-9	7	—	8.5	14	13-15	1
Alice	9	6-12	—	—	9	20	19-21	1
Work	none	—	0	0	0	10	9-11	1
Kildala	none	—	5	6	5	11	10-12	1
Douglas	5	3-7	0	3	6.5	17	9-21	4
Gardner	6	4.5-7	1	4	6.5	10	9.5-10.5	1
Surf	none	—	0	0	0	0.5	0-1	1
Laredo	none	—	0	0	0	4.5	0-8	1
Sheep	none	—	0	0	1.5	8	0-18	1
Kynoch	none	—	0	0	0	8	4-11	1
Spiller	4	...	0	0	4	9	6-12	1
Briggs	none	—	0	0	—	4	2-6	1
Roscoe	none	—	2.5	0.5	2	6	5-7	1
Cascade	none	—	5	5	7	12	11-13	1
Dean	6	5.5-6.5	3	7	7	13	11-14	2
Burke	5	4.5-7	0	0.5	6	10	8-12	2
S. Bentinck	8	7.5-9	7.5	—	10	13	...	1
Moses	2	1.5-3	4	4.5	4.5	8.5	7.5-10	2
Rivers	2	1.5-3	0.5	3	3.5	6.5	5-8.5	2
Draney	1.5	1.5	0	1.5	2.5	7	6.5-8	1
Smith	1.5	1.5	0	—	2.5	5	...	1
Belize	0.5	0-1	0	1	0	6	3.5-8.8	1
Seymour	none	—	0	1	3	10	6.5-12	1
Kingcome	3	2.5-3.5	—	3	3.5	8	6.5-10	3
Knight	5	3-7	0	5.5	6.5	12	10-14.5	7
Call	6	5-7	0	—	0	0	...	3
Loughborough	1.5	1-3	0.5	—	2	3	2.5-4.5	3
Bute	4.5	3-6	0.5	4	5.5	9.5	7-14	12
Toba	2	1.5-3.5	2	—	3.5	15	9-20	5
Pendrell	none	—	0	—	0	11	6-18	5
Jervis	none	—	0	1	2	15	7-21	6
Sechelt	1.5	...	0	0	1.5	24	20-30	1
Howe	6	...	4	5	7	10	10-11	1
Indian	2	1-4	0	1	1	25	20-30	8

the depth of the layer decreases somewhat from the head toward the mouth. Eventually the salinity-depth profile becomes so rounded that it is difficult to select a specific depth for the layer. The homogeneous layer sometimes observed near the mouth (Type 1c profile) is generally much deeper than that at the head and is of much greater salinity.

The depth at which the salinity reaches 50 and 90% respectively of the base salinity may be read without ambiguity from the salinity-depth profiles. In the inlets with considerable runoff the 50% depth is not more than 2 m greater than that of the homogeneous layer. It decreases from head to mouth of an inlet, and in most cases is at or close to the surface at the mouth. The chief exceptions are those inlets which terminate part way along another inlet (e.g. Observatory opening into Portland, South Bentinck opening into Burke).

The 90% depth does not show the same regular decrease toward the mouth. In many cases, the 90% depth is relatively constant from station to station in

the inner half of an inlet but fluctuates considerably in the outer half. The values in Table IV indicate the mean value and the range of values observed for each inlet as a whole.

Occasional salinity inversions have been noted, usually toward the heads of inlets between the surface sample (taken with a bucket) and the next below it (taken with a water sampling bottle). These inversions are considered only to be significant of a cloudy structure in the water which is to be expected in the immediate vicinity of river inflow.

3.14 TEMPERATURE DISTRIBUTION WITH DEPTH IN THE SHALLOW ZONE

It is generally true that the shallow-zone temperature profile with depth is qualitatively a mirror image about a vertical axis of the salinity profile if both are plotted in the conventional manner with both temperature and salinity increasing to the right (e.g. Fig. 9 and 10). That is to say, an inlet with a salinity profile of Type 1 (Fig. 15) will have an isothermal layer below which there is a thermocline and then a reduced temperature gradient. With Type 2 salinity profiles the temperature generally decreases with depth from the surface, the gradient decreasing as the depth increases, e.g. Fig. 11.

In the Type 1 salinity profile inlets the thermocline is closely associated in depth with the halocline. In order to examine this association, a series of casts was made in Knight in 1955 with closely spaced Fjarlie water sampling bottles while a cast was made with a 20-m range bathythermograph close to the bottles as the messenger was dropped. A selection of salinity and temperature profiles from this series is shown in Fig. 16. The minimum water bottle spacing practicable with the 0.3-m-long Fjarlie bottles was 1 m and attempts were made to arrange a closely spaced group of bottles in the thermocline as determined from a preliminary bathythermograph cast. The bathythermograph used had only a small

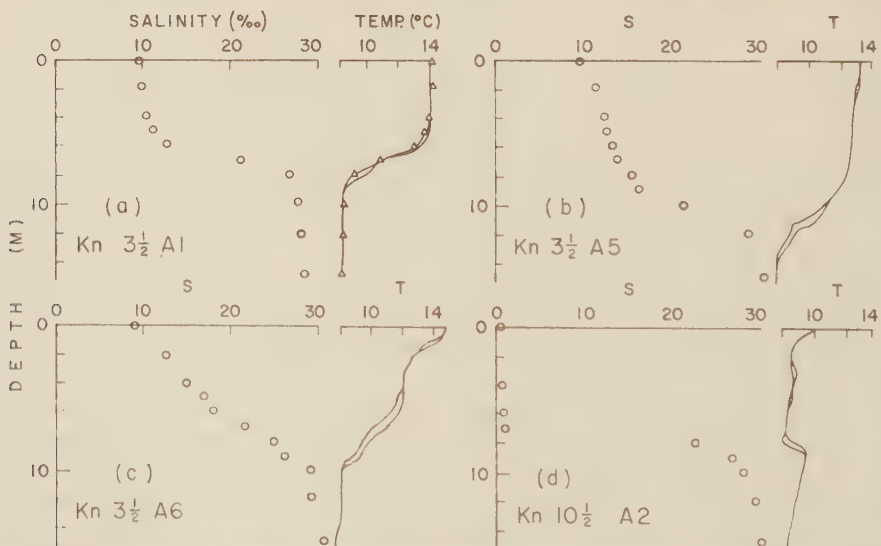


FIG. 16. Observations of salinity and temperature closely spaced in depth in Knight Inlet.

hysteresis, and previous and subsequent comparisons with reversing thermometers showed it to be a reliable instrument. The reversing thermometer temperatures observed are shown as an example in Fig. 16(a). It is clear from Fig. 16 that within the limitations imposed by the discrete character of the salinity observations the halocline and thermocline coincide in depth.

The T-S diagram corresponding to Fig. 16(a) is shown in Fig. 17. It is an excellent example of a water mass resulting from the mixing of only two water

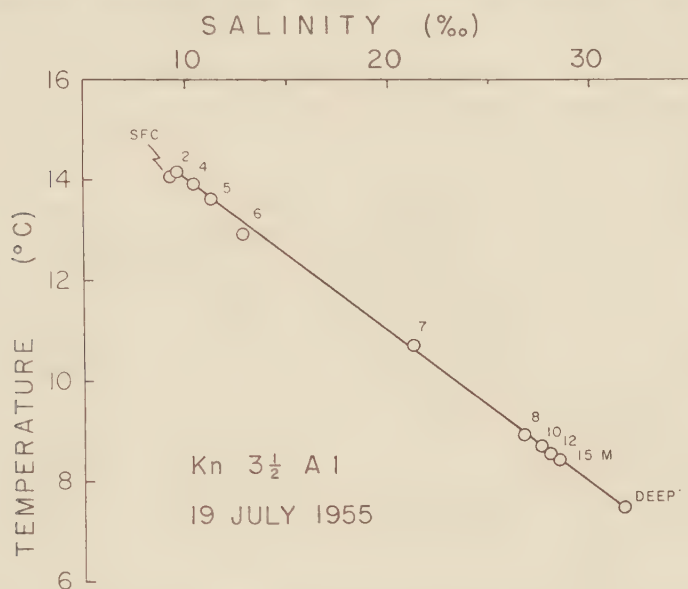


FIG. 17. Temperature-salinity diagram for Sta. Knight 3 1/2 A (cf. Fig. 16(a)).

types, the low-salinity warm surface layer of 2 to 3 m depth with the cooler, more saline deep water.

The profiles in Fig. 16(d) were obtained near the head of Knight, and the surface layer of low-salinity water was cold as it had just entered the inlet from a river originating in glaciers. The sharp increase in temperature at 8 to 9 m depth is seen to be substantially coincident with the very sharp halocline.

The data of which the profiles in Fig. 16 are representative indicate that when a pronounced halocline and thermocline are both present the two agree closely in depth. However, neither is necessarily found with the other. Near the head of a large-runoff inlet with a conspicuous halocline there may be no significant thermocline (although irregularities in the temperature-depth profile are often present in such a case). In low-runoff inlets the shallow zone may have a marked thermocline even when the water is almost isohaline. It is, in fact, not practical to divide the inlets into types in terms of temperature profiles as has been done for salinity. This is the opposite of the open ocean situation where it is easier to categorize the temperature profiles than the salinity profiles.

The reason for the variety of combinations of temperature-depth and salinity-depth profiles found is that the stratification in the shallow zone is dominated

by the effect of salinity on density, with temperature playing a minor or even insignificant role. In the large-runoff inlets the fresh water at the head, on entry from the rivers, is at or below the temperature of the cool deeper saline water. It forms a low-density surface layer and as this flows along the inlet it absorbs heat from the sun and atmosphere and its temperature therefore rises and a thermocline develops. Mixing with the underlying saline water occurs during the passage along the inlet and the stability of the water diminishes; mixing then takes place over greater depths and the intensity of both halocline and thermocline decreases. Therefore while most marked haloclines are found at the heads of the large-runoff inlets, the most marked thermoclines are found toward mid-length of the inlets.

3.2 DEEP ZONE

3.21 MAIN FEATURES OF SALINITY AND TEMPERATURE DISTRIBUTIONS

In the characteristics of the deep water (20 m and deeper) there is a marked gradation from south to north along the coast. In the southern inlets the salinity is lower and the temperature higher at the same depths than in the northern ones. The southern inlets include those from Indian to Loughborough. The northern inlets include Smith and all those north of it except for two side arms, Moses and Alice. Call, Knight, Kingcome, Draney and Moses in the mid-coast region have deep water with characteristics intermediate between those of the southern and northern groups. The water characteristics in Seymour and Belize fall into the southern group category, while Alice has salinities similar to the intermediate group but lower temperatures than in other inlets in the north. Possible explanations for these differences are offered and discussed later.

Mean values of temperature and salinity are summarized in Table V for comparison. The mean values are also displayed in the diagrams of Fig. 18 for

TABLE V. Mean values of subsurface temperature and salinity of the water in the inlets of the British Columbia mainland coast.

Inlets	Depth									
	20 m		50 m		100 m		200 m		400 m	
	T	S	T	S	T	S	T	S	T	S
	°C	‰	°C	‰	°C	‰	°C	‰	°C	‰
Northern group:	7	31.0	6.5	32.0	6.5	32.7	6.3	33.0	6.3	33.2
Except:										
Alice	6.5	29.0	5.5	30.5	5.2	31.0	4.3	31.4	-	-
Surf and Laredo	10	31.5	8.0	32.0	...	...	...	...	-	-
Intermediate group:	8	29.5	7.0	30.5	6.6	30.8	7.3	31.2	7.3	31.2
Except:										
Moses	...	...	7.1	31.5	7.1	31.6	7.3	32.0	-	-
Southern group:	8	29.0	8.0	29.5	7.5	30.0	8.1	30.5	8.3	30.7
Except:										
Seymour	8	28.5	7.3	28.8	7.4	29.0	7.8	29.0	7.4	29.0
Princess Louisa	11	23.5	8.8	26.5	7.7	28.2	-	-	-	-
Sechelt	11	26.0	8.8	27.5	7.5	28.5	7.4	28.6	-	-
Indian	11	25.5	10.0	26.4	7.9	27.2	7.0	27.2	-	-

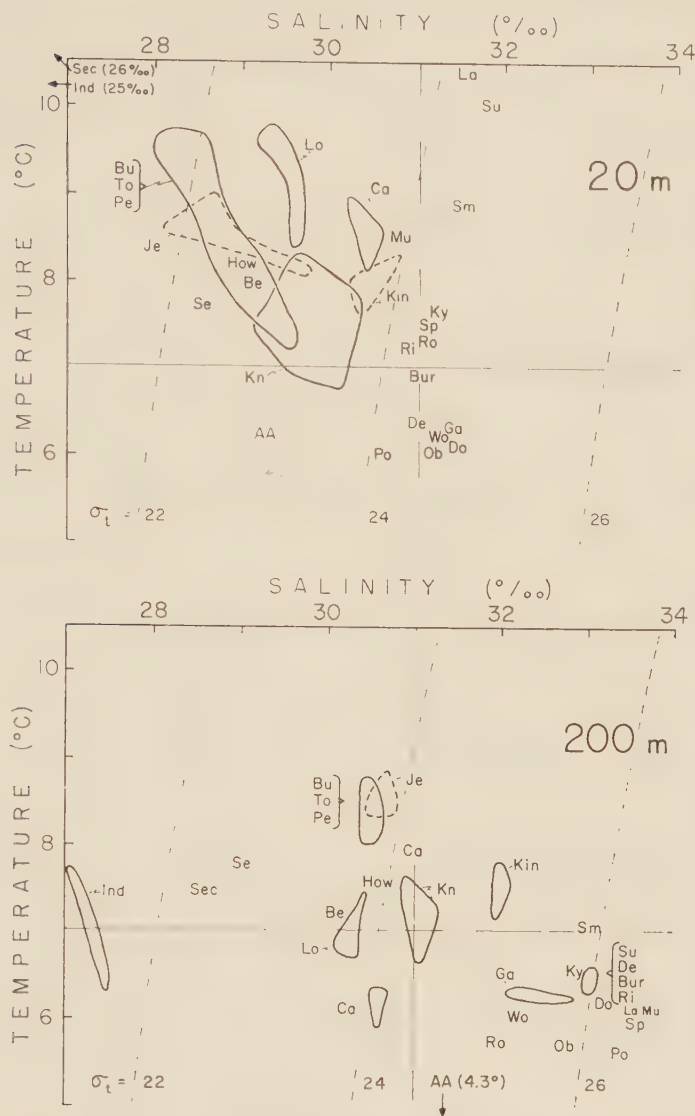


FIG. 18. Summary of temperature-salinity characteristics of the water at 20 and 200 m depth in British Columbia mainland inlets.

depths of 20 and 200 m which are considered to be sufficiently representative of the upper and lower parts of the deep zone.

The latter diagrams clearly show the difference in water characteristics between the southern and northern inlets. The mean difference in temperature is 1 to 1.5 C degrees and in salinity is 2 to 2.5‰. The wider distribution of temperature at 20 m than below this depth is attributed to climatic effects.

More detailed values of salinity and temperature are given in Tables VI and VII. In these are listed for depths of 20 m and greater for each cruise for each

TABLE VI. Mean values of salinity (‰) along the length of each inlet for each cruise, with range of salinity about mean which includes at least 75% of all values for each cruise (Note 1).

Inlet	Date	DEPTH (METRES)							(Notes)
		20	50	100	200	300	400	500	
Portland C.	Jul. 51	30.7±1.0	32.0±0.2	32.8±0.2	33.1±0.2	33.34	33.40	—	—
Observatory	Jul. 51	30.8±0.8	32.0±0.2	32.6±0.3	32.66	...	32.66	...	—
Hastings	Jul. 51	30.5±0.1	31.86	32.10	32.14	—	—	—	—
Alice	Jul. 51	29.4±0.8	30.7±0.1	30.96	31.32	...	—	—	—
Work	Jul. 51	31.3±0.3	31.8±0.1	31.96	32.10	32.14	—	—	—
Douglas	Jul. 51	31.5±0.3	32.3±0.3	32.9±0.1	33.2±0.2	...	33.32	—	—
	Jun. 52	30.5±0.1	31.7±0.1	32.4±0.1	32.7±0.1	...	...	—	(2)
	Jul. 52	30.7±0.4	31.9±0.2	32.6±0.2	32.7	...	...	—	(2)
	Aug. 52	31.1±0.7	31.8±0.2	32.6	32.96	...	...	—	(2)
	Aug. 54	31.2±0.1	31.9±0.2	32.76	33.0±0.1	33.08	33.24	—	(3)
Kildala	Jul. 51	31.6±0.1	32.00	32.86	...	—	—	—	—
Gardner	Jul. 51	31.6±0.4	31.9±0.1	32.0±0.1	32.2±0.1	...	33.16	—	(4)
		...	...	32.4±0.2	32.5	...	...	—	(5)
	Aug. 54	31.2±0.5	31.8±0.2	32.8±0.1	33.7	...	33.3±0.1	—	(6)
				32.2±0.1	32.4±0.2	33.00	...	—	(7)
Surf	Jul. 51	31.8±0.1	32.3±0.1	32.9±0.1	33.06	...	—	—	—
Laredo	Jul. 51	31.5±0.2	32.2±0.1	33.2±0.2	33.4±0.1	33.46	—	—	—
Sheep	Jul. 56	30.5±0.4	31.8±0.2	33.10	33.30	33.36	—	—	—
Kynoch	Jul. 56	31.0±0.2	32.26	32.76	32.86	32.96	32.98	32.98	33.04
Spiller	Jul. 56	31.1±0.5	32.0±0.2	33.2±0.2	33.40	33.42	...	—	—
		...	...	32.8	33.0	...	...	—	(8)

	Jul. 56	29.4	29.8	...	...	...	...	...	...	...
Briggs	Jul. 56	30.0	31.5±0.1	31.9	...	...	...	...	...	...
Roscoe	Jul. 56	30.0	31.5±0.1	31.9	...	...	...	...	...	...
Dean	Jun. 51	31.0±0.3	31.9±0.1	32.8±0.2	33.1	33.1	33.1	33.1	33.1	...
	Jul. 56	30.7±0.2	31.6±0.2	32.6±0.1	33.0±0.1	33.0±0.1	33.0±0.1	33.0±0.1	33.0	...
Cascade	Jul. 56	30.8	31.8±0.1	32.66	32.86	32.98	32.98	32.98	32.98	...
Burke	Jun. 56	31.1±0.8	32.1±0.4	32.8±0.1	33.0±0.1	33.05	33.10	33.10	33.10	...
	Jul. 56	30.7±0.4	31.8±0.2	32.6±0.1	32.9±0.1	33.0±0.1	33.08	33.08	33.2	...
Kwatna	Jul. 56	30.9	31.7	32.5	32.9	32.9	33.0	33.0	33.0	...
S. Bentineck	Jun. 51	30.6±0.2	32.0±0.1	32.7±0.1	33.0	33.1	...	...	...	...
Rivers	Jun. 51	30.8±0.3	31.8±0.1	32.8±0.1	33.06	33.10	33.10	33.10	33.10	...
	Jul. 56	31.1±0.2	32.0±0.1	32.8±0.1	33.06	33.06	33.06	33.06	33.06	...
Moses	Jun. 51	30.7	31.5	31.6	31.7	31.7	31.7	31.7	31.7	...
	Jul. 56	30.6	31.3	31.7	31.9	31.9	31.9	31.9	31.9	...
Draney	Jun. 51	29.4±0.2	30.0±0.1	30.80	...	...	...	...	...	...
Smith	Jul. 55	31.5±0.2	32.2±0.2	32.9±0.1	33.0	33.0	33.0	33.0	33.0	...
Belize	Jun. 51	29.3±0.2	29.8±0.2	30.0±0.1	30.1±0.1	30.1	30.1	30.1	30.1	...
Seymour	Jun. 51	28.4±0.1	28.8±0.1	28.8±0.1	29.0	29.0	29.0	29.0	29.0	...
Drury	Jul. 55	29.9	30.1	...	...	...	...	...	...	...
Kingcome	Jul. 53	30.2±0.1	30.7±0.1	31.5±0.1	31.9±0.1	32.0	32.0	32.0	32.0	...
	Jul. 55	30.8	31.2±0.1	31.80	31.98	32.00	32.00	32.00	32.00	...
	Jun. 57	30.3±0.1	30.8±0.2	31.40	31.78	32.1±0.1	32.2	32.2	32.2	...
Knight	Jun. 51	29.3±0.5	30.6±0.1	30.8±0.1	31.0	31.1	31.16	31.16	31.18	(9)
		30.0±0.3	30.8±0.1	31.3	31.5	...	...	...	...	...
	Jun. 52	30.0±0.3	30.7±0.2	30.7±0.1	31.0	31.2	31.3	31.3	31.3	...
		30.5	31.0	31.3	...	...	...	...	...	...

TABLE VI.—Continued

Inlet	Date	DEPTH (METRES)							600
		20	50	100	200	300	400	500	
Knight (Cont.)	Jul. 53	29.8±0.5	30.4±0.2	30.9±0.2	31.0±0.1	31.0±0.1	31.1±0.1	31.1	(Notes)
		30.1±0.3	30.9±0.1	31.1±0.2	31.5±0.1	—	—	—	—
	Jul. 55	30.3±0.3	30.9	31.14	31.20	31.22	31.24	31.26	—
		30.6±0.1	31.1±0.1	31.76	...	—	—	—	—
	Jul. 56	29.0±0.5	30.4±0.1	30.7±0.2	31.0±0.1	31.1±0.1	31.2±0.1	31.26	—
		29.6±0.9	30.9	31.2±0.1	...	—	—	—	—
	Jun. 57	30.0±0.1	30.7±0.1	30.9±0.1	31.06	31.18	31.24	31.28	—
		30.4±0.2	30.9±0.2	31.2±0.1	31.4	—	—	—	—
	Sep. 57	29.5±0.5	30.3±0.2	30.6±0.1	30.9±0.1	30.9	30.96	...	(10)
		30.0±0.5	30.86	31.42	31.48	—	—	—	—
Call	Jun. 58	29.6±0.1	30.3±0.1	30.62	30.86	31.04	31.12	...	—
		29.95	30.6	31.3	...	—	—	—	—
	Jun. 59	29.8±0.1	30.5±0.1	30.66	30.90	31.00	31.10	31.10	—
		30.24	30.72	31.22	...	—	—	—	—
	Jul. 53	30.4	30.7	30.7	...	—	—	—	—
	Aug. 53	30.4±0.1	30.66	30.76	30.96	—	—	—	—
	Jul. 55	30.5	30.8±0.1	30.9	31.0	—	—	—	—
	Jul. 56	30.2	30.40	30.42	30.5	—	—	—	—
	Jun. 57	30.4±0.1	30.64	30.66	30.7	—	—	—	—
	Sep. 57	30.2	30.50	30.46	...	—	—	—	—
Loughborough	Jul. 53	29.4±0.2	29.6±0.1	30.1±0.1	30.36	—	—	—	—
	Jul. 55	29.6	29.8±0.1	30.3	30.5	—	—	—	—
	Jul. 56	29.2±0.1	29.50	29.98	30.16	—	—	—	—
	Jun. 57	29.6±0.1	29.9±0.2	30.08	30.30	—	—	—	—
	Sep. 57	29.3±0.1	29.5±0.2	29.8±0.2	30.08	—	—	—	(10)
	May 51	29.0±0.4	29.2±0.2	29.9±0.2	30.4±0.1	30.5±0.1	30.5±0.1	30.5±0.1	30.6
	Aug. 51	28.3±0.2	29.1±0.1	30.1±0.1	30.5±0.1	30.5	...	...	...
	Oct. 51	28.8±0.1	29.3±0.2	30.1±0.2	30.4±0.1	...	30.56	30.58	...
Bute	Mar. 52	29.0±0.8	29.8±0.2	30.0±0.2	30.6±0.1	30.6±0.1	30.70	30.70	...
	May 52	29.3±0.2	29.6±0.2	30.2±0.1	30.52	30.56	30.56	30.60	...

Aug. 52	28.7 ± 0.2	29.4 ± 0.1	30.2 ± 0.1	30.6 ± 0.1	30.60	30.62	30.7	...
Mar. 53	29.1 ± 0.2	29.4 ± 0.1	29.9 ± 0.1	30.6 ± 0.1	30.6	30.7	30.7	30.7
Jul. 53	28.3 ± 0.6	29.3 ± 0.2	30.3 ± 0.2	30.7 ± 0.1	30.6 ± 0.1	30.6	30.6	...
Aug. 53	28.7 ± 0.3	29.2 ± 0.2	30.2 ± 0.2	30.6 ± 0.1	30.7 ± 0.1	30.74	30.76	30.78
Jan. 54	28.8 ± 0.2	29.5 ± 0.3	29.9 ± 0.1	30.4	30.62	...	...	...
Jul. 55	28.5 ± 0.3	29.7 ± 0.1	30.3 ± 0.2	30.6 ± 0.1	30.6	30.6 ± 0.1	30.7	30.7
Jul. 56	28.6 ± 0.2	29.3 ± 0.1	30.2 ± 0.1	30.4 ± 0.1	30.5 ± 0.1	30.56	30.58	30.58
May 57	29.5 ± 0.2	29.8 ± 0.2	30.2 ± 0.2	30.64	30.66	30.68	30.68	30.66
Jul. 57	28.5 ± 0.2	29.4 ± 0.2	30.2 ± 0.1	30.5 ± 0.1	30.62	30.64	30.64	30.66
Sep. 57	28.1 ± 0.3	29.0 ± 0.1	30.0 ± 0.1	30.28	30.34	30.36	30.38	(10)
Nov. 57	29.0 ± 0.2	29.5 ± 0.1	30.0 ± 0.1	30.48	30.48	30.52	30.54	30.64
Feb. 58	29.1 ± 0.3	29.6	30.1 ± 0.1	30.6 ± 0.1	30.62	30.64	30.66	30.68
Mar. 58	28.7 ± 0.3	29.2 ± 0.1	29.6 ± 0.1	30.5 ± 0.1	30.60	30.62	30.64	...
May 58	28.9 ± 0.1	29.4 ± 0.1	29.8 ± 0.1	30.38	30.54	30.56	...	...
Jun. 58	28.2 ± 0.2	28.96	30.00	30.46	30.56	30.62	30.62	30.64
Jun. 59	28.6 ± 0.1	29.3 ± 0.1	29.90	30.40	30.48	30.50	30.56	30.56
Jun. 60	28.3 ± 0.3	29.1 ± 0.2	30.0 ± 0.2	30.5	30.56	30.6	30.62	30.62
Ramsay								
Jun. 54	28.7	29.5	30.1	30.4	30.6	-	-	-
Jun. 56	28.0	29.4	30.1	30.4	30.5	-	-	-
Toba								
Aug. 51	28.6 ± 0.1	29.2 ± 0.1	30.0	30.5	...	30.5	...	-
Mar. 53	29.1 ± 0.1	29.4 ± 0.2	30.0 ± 0.1	30.5 ± 0.1	30.6 ± 0.1	30.7	30.7	-
Jun. 54	28.5 ± 0.1	29.6 ± 0.1	30.04	30.38	30.5	...	...	-
Jun. 55	27.4 ± 0.1	29.8 ± 0.1	30.4	30.6	30.6	30.6	30.6	-
Jun. 56	28.1 ± 0.4	29.7 ± 0.2	30.28	30.52	30.56	30.58	30.64	-
Sep. 57	28.4 ± 0.4	29.3 ± 0.1	30.2 ± 0.1	30.48	30.52	...	...	-
Feb. 58	28.5 ± 0.2	29.3 ± 0.1	30.16	30.5 ± 0.1	30.56	30.58	...	-
Mar. 58	28.1 ± 0.4	29.1 ± 0.1	29.76	30.46	30.54	30.56	...	-
May 58	28.9 ± 0.1	29.4 ± 0.1	29.86	30.36	30.54	30.56	...	-
Jun. 58	28.3 ± 0.1	29.5 ± 0.2	29.98	30.44	30.54	30.62	...	-
Pendrell								
May 51	28.8 ± 0.1	29.5 ± 0.1	30.1	30.5	...	...	-	-
Aug. 51	28.9 ± 0.1	29.2 ± 0.1	30.1	30.5	...	...	-	-
Mar. 53	28.9 ± 0.2	29.4	30.1	30.6	30.7	30.7	-	-
Jul. 53	28.5	29.3 ± 0.1	30.2	30.5	30.6	...	-	-
Aug. 53	28.0 ± 0.2	29.2 ± 0.1	30.2 ± 0.1	30.66	30.70	...	-	-

TABLE VI.—Continued

Inlet	Date	DEPTH (METRES)								(Notes)
		20	50	100	200	300	400	500	600	
Pendrell (Cont.)	Jun. 54	28.7 ± 0.2	29.6 ± 0.1	30.10	30.44	30.5	...	—	—	
	Jun. 56	28.1	29.34	30.16	30.46	30.56	...	—	—	
	Sep. 57	28.3 ± 0.1	29.28	30.10	30.54	30.5	...	—	—	
Jervis	May 52	29.9 ± 0.2	30.3 ± 0.2	30.5 ± 0.2	30.88	31.04	31.1	31.1	31.1	
	Jun. 54	28.4 ± 0.5	30.0 ± 0.1	30.2 ± 0.1	30.58	30.82	...	...	...	
	Jun. 56	28.1 ± 0.2	29.6 ± 0.2	29.8 ± 0.3	30.5 ± 0.2	30.6	30.6 ± 0.1	30.68	30.7	
	May 57	28.5 ± 0.4	30.2 ± 0.1	30.4 ± 0.1	30.76	30.94	31.08	31.12	31.08	
	Jul. 57	28.7 ± 0.1	29.7 ± 0.1	30.1 ± 0.1	30.7 ± 0.1	30.9 ± 0.1	30.98	31.04	31.04	
	Nov. 57	28.8 ± 0.4	29.8 ± 0.4	30.3 ± 0.3	30.7 ± 0.1	30.8 ± 0.1	30.86	30.92	30.94	
	Feb. 58	28.0 ± 0.2	29.6 ± 0.2	30.1 ± 0.1	30.6 ± 0.2	30.9 ± 0.1	30.98	30.98	31.00	
	May 58	28.7 ± 0.1	29.58	29.86	30.48	30.78	30.92	...	...	
	Jun. 58	28.5 ± 0.4	29.64	29.98	30.48	30.78	30.92	30.94	30.96	
	Jun. 59	27.5 ± 0.2	29.76	30.18	30.68	30.86	30.94	30.98	31.00	
	Jun. 60	29.0 ± 0.5	29.9 ± 0.1	30.2 ± 0.1	30.7	30.88	30.94	30.96	30.98	
	Pr. Louisa	May 52	23.6	27.2	28.8	...	—	—	—	—
Jun. 60		22.8	26.1	28.2	28.2 at 176 m	—	—	—	—	
Sechelt	Jul. 57	25.8 ± 0.2	27.5 ± 0.2	28.46	28.58	—	—	—	—	
	Mar. 53	29.7 ± 0.2	30.3 ± 0.2	30.5 ± 0.1	30.6	...	—	—	—	
Howe	Jun. 57	29.2 ± 0.1	29.8 ± 0.1	30.2 ± 0.2	30.5 ± 0.2	...	—	—	—	
	Jun. 53	24.8 ± 0.2	26.6 ± 0.4	27.8	...	—	—	—	—	
Indian	Sep. 53	26.3 ± 0.3	26.7 ± 0.2	27.9	28.0	—	—	—	—	
	Win. 56	26.0 ± 0.3	26.6 ± 0.3	27.2 ± 0.2	27.3 ± 0.1	—	—	—	(11)	
	Sum. 56	26.4 ± 0.5	26.6 ± 0.2	27.2 ± 0.2	27.4	—	—	—	—	
	Win. 57	26.9 ± 0.3	27.1 ± 0.3	27.3 ± 0.2	27.4 ± 0.3	—	—	—	—	
	Sum. 57	25.4 ± 1.0	26.2 ± 0.3	27.3 ± 0.2	27.5 ± 0.1	—	—	—	—	
	Win. 58	26.3 ± 0.5	26.8 ± 0.3	27.2	27.3	—	—	—	—	
	Sum. 58	25.2 ± 0.8	26.1 ± 0.3	27.1 ± 0.1	27.3	—	—	—	—	
	Win. 59	26.1 ± 0.7	26.5 ± 0.4	26.9 ± 0.2	27.1 ± 0.1	—	—	—	—	
	Sum. 59	25.0 ± 1.0	26.1 ± 0.1	26.9 ± 0.1	27.1 ± 0.1	—	—	—	—	

Notes:

- (1) When the $\pm$ range including at least 75% of the values at a particular depth ("75% range") was 0.02‰ or less its value has been omitted and the mean salinity quoted to the nearest 0.02‰. When the "75% range" was between 0.03 and 0.07‰ its value has been omitted and the mean salinity quoted to the nearest 0.1‰. When the "75% range" was 0.08‰ or over its value has been quoted to the nearest 0.1‰.
- (2) Data collected by Canadian Hydrographic Service.
- (3) Data collected by Pacific Oceanographic Group, Sta. Do 6, 8 and 10 only.
- (4) Stations Ga 4-14 at 50 m, Ga 8-14 at 100, 200 and 400 m.
- (5) Stations Ga 3-7 at 100, 200 m.
- (6) Stations Ga 1 and 2 at 50 m and deeper.
- (7) Data collected by Pacific Oceanographic Group, Sta. Ga 4, 6 and 10 only.
- (8) Station Sp 5 only.
- (9) For Knight Inlet for each cruise the first line of data refers to Sta. 4-11 inside the sill, and the second line to Sta. 1-3 outside the sill.
- (10) The salinity data for Bute, Loughborough and Knight for the cruise of September 1957 appear to be low by about 0.25‰ compared to values on previous and later cruises and should be regarded with caution.
- (11) The information available for Indian Arm for 1956 to 1959 is more extensive than for any other inlet (36 cruises) and is the subject of a separate study (Gilmartin, 1960). Here it has been summarized in two groups each year: June to October (Summer) and November to May (Winter).

inlet the mean values together with a value referred to as the "75% range". The 75% range in Tables VI and VII is a range, above and below the mean value, which includes at least 75% of the values for the particular inlet and depth. It is intended simply as an indication of the range of values experienced, the number of values available being so variable and in many cases so small that the calculation of standard deviations would be of doubtful significance.

These Tables show clearly the change in salinity and temperature from north to south, and also show that both seasonal and year-to-year changes evidently occur.

The most noticeable change with location is the decrease in salinity and increase in temperature which occurs in the region between Smith and Knight. The details of this change, together with a comparison of water characteristics and topography, lead to possible explanations of the north-south variation in which both meteorological and oceanographic conditions play their part. The mean annual air temperature differences between south and north are not large, since the annual mean isotherms are only slightly inclined to the coastline. However from south to north there is a decrease in mean air temperature of the order of 3 C degrees (Thomas, 1953; Kendrew and Kerr, 1955) which must contribute to the observed decrease in mean water temperature to the north.

Nordgaard (1903) states that in Norwegian fjords with shallow sills the deep water temperature is close to the mean air temperature in the region, indicating a long-term climatic influence.

The annual precipitation, on the other hand, does not show a similar south to north decrease. In fact the areas of highest precipitation are north of Smith (Thomas, 1953; Chapman and Turner, 1956). It seems more likely that the variation of deep water salinity is associated with the directness or otherwise of the connection to the Pacific (as the source of the most saline water). The inlets from Smith to the north have deep sills and connect more or less directly through Hecate Strait to the Pacific at depths of the order of 130 m and through Dixon Entrance at depths of 160 m for the most northerly inlets. On the other hand the inlets from Bute southward open into the Strait of Georgia. This receives considerable quantities of fresh water runoff from several rivers; it is almost closed to the north and has only restricted connection at the south end with the Pacific. Since the salinities in Hecate Strait are 2 to 3‰ greater at the same depths than in the Strait of Georgia (e.g. Pacific Oceanographic Group, 1955; Waldichuk, 1957) a corresponding difference is to be expected between the northern and southern inlets.

The local differences in the Smith-Knight region previously mentioned may be seen in Table VI. Smith, with a moderately deep sill and opening directly to Queen Charlotte Sound and the Pacific Ocean, has a salinity at 200 m of 33.0‰. In Knight with a shallower sill and a less direct connection to the Pacific the salinity at 200 m is only 31.2‰. Kingcome which has a deeper sill than Knight and is between the previous two has a salinity of 32.0‰. Belize and Seymour, between Smith and Kingcome, show lower values than any of these (29 and 28‰ respectively). These two inlets have a common shallow sill which restricts the

TABLE VII. Mean values of temperature ($^{\circ}\text{C}$) along the length of each inlet for each cruise, with range of temperature about mean which includes at least 75% of all values for that cruise.

Inlet	Date	DEPTH (METRES)							(Notes)
		20	50	100	200	300	400	500	
Portland C.	Jul. 51	6.9 ± 1.4	5.8 ± 0.7	5.6 ± 0.1	5.6 ± 0.1	5.6 ± 0.1	5.63	—	—
Observatory	Jul. 51	6.8 ± 0.8	5.8 ± 0.3	5.5 ± 0.1	5.7 ± 0.1	...	5.72	...	—
Hastings	Jul. 51	6.0 ± 0.1	5.31	5.61	5.62	—	—	—	—
Alice	Jul. 51	6.5 ± 0.4	5.3 ± 0.1	5.3 ± 0.2	4.30	...	—	—	—
Work	Jul. 51	6.1 ± 0.4	5.8 ± 0.1	5.9 ± 0.1	5.95	5.95	—	—	—
Douglas	Jul. 51	6.2 ± 0.6	6.5 ± 0.2	6.2 ± 0.1	6.20	6.16	6.02	—	—
	Jun. 52	6.2 ± 0.7	6.2 ± 0.7	6.7	6.4	...	...	—	(2)
	Jul. 52	6.6 ± 0.3	6.4 ± 0.3	6.7	...	...	...	—	(2)
	Aug. 52	8.9 ± 1.5	7.1 ± 1.2	6.7 ± 0.1	6.4	...	...	—	(2)
Aug. 54	Aug. 54	7.5 ± 0.1	7.3	6.8	6.7	6.68	6.64	—	(3)
Kildala	Jul. 51	5.9 ± 0.2	6.5 ± 0.2	6.18	...	—	—	—	—
Gardner	Jul. 51	6.4 ± 0.3	6.3 ± 0.1	6.3 ± 0.1	6.4 ± 0.1	...	6.48	—	(4)
	Aug. 54	7.4 ± 0.1	7.2 ± 0.1	7.1	7.1 $\pm$ 0.1	7.13	6.10	—	(5)
	Jul. 51	10.3 ± 1.5	8.0 ± 0.4	6.7 ± 0.1	6.40	...	...	—	(6)
Laredo	Jul. 51	10.0 ± 1.5	7.5 ± 0.6	6.54	6.20	6.00	—	—	—
Sheep	Jul. 56	7.9 ± 0.7	6.7 ± 0.5	6.2 ± 0.1	6.09	6.07	—	—	—
Kynoch	Jul. 56	7.6 ± 0.6	6.3 ± 0.3	6.4 ± 0.2	6.5 ± 0.1	6.65	6.66	6.66	6.67
Spiller	Jul. 56	7.7 ± 1.0	6.9 ± 0.3	6.4 ± 0.1	6.05	...	...	—	—
	...	...	...	6.98	6.99	...	...	—	(7)
Briggs	Jul. 56	9.4	7.9	...	...	...	...	...	...
Roscoe	Jul. 56	7.3 ± 0.4	5.8 ± 0.1	5.8 ± 0.2	...	—	—	—	—
Dean	Jun. 51	6.0 ± 0.8	6.4 ± 0.3	6.6 ± 0.2	6.5 ± 0.1	6.4 ± 0.1	6.48	6.47	—
	Jul. 56	5.5 ± 1.0	6.5 ± 0.7	6.5 ± 0.4	6.4 ± 0.2	6.3 ± 0.1	6.5 ± 0.3	6.4 ± 0.2	—

TABLE VII.—Continued

Inlet	Date	DEPTH (METRES)							(Notes)
		20	50	100	200	300	400	500	
Cascade	Jul. 56	5.6±0.2	5.8±0.2	6.5	6.4±0.1	6.7	—	—	—
Burke	Jun. 51	7.2±0.6	6.9±0.3	6.6±0.2	6.5±0.1	6.50	6.46	6.38	—
	Jul. 56	6.9±1.1	5.6±0.6	6.6±0.2	6.5±0.2	6.4±0.2	6.6±0.1	6.65	—
Kwatna	Jul. 56	6.4	5.1	6.0	6.6	6.6	6.7	...	—
S. Bentinck	Jun. 51	7.1±0.2	6.5±0.1	6.6±0.1	6.5±0.1	...	6.45	—	—
Rivers	Jun. 51	7.4±0.2	7.1±0.2	6.9±0.2	6.5±0.1	6.45	—	—	—
	Jul. 56	7.1±0.2	6.9±0.2	6.6±0.2	6.4±0.2	6.28	—	—	—
Moses	Jun. 51	7.6±0.2	7.1±0.1	7.0	6.95	—	—	—	—
	Jul. 56	7.3	7.0	7.0	7.7	—	—	—	—
Draney	Jun. 51	7.9±0.2	7.8±0.2	6.9±0.1	—	—	—	—	—
Smith	Jul. 55	8.9±0.1	7.6±0.1	7.1±0.1	7.0±0.1	...	—	—	—
Belize	Jun. 51	8.2±0.8	7.8±0.7	7.5±0.4	7.4±0.3	7.04	—	—	—
Seymour	Jun. 51	7.7±0.5	7.3±0.3	7.4±0.3	7.9±0.1	7.93	7.45	7.35	7.35
Drury	Jul. 55	9.7	9.3	—	—	—	—	—	—
Kingcome	Jul. 53	8.0±0.6	7.3±0.3	7.48	7.9±0.2	7.52	...	—	—
	Jul. 55	8.3±0.1	7.6±0.2	7.5±0.1	7.56	7.53	...	—	—
	Jun. 57	7.8±0.3	6.8±0.1	6.8±0.1	7.2±0.2	7.53	7.58	—	—
Knight	Jun. 51	7.3±0.5	6.6±0.4	6.6±0.1	6.7±0.1	6.80	6.83	6.88	(8)
	Jun. 52	7.0±0.5	7.1±0.4	6.9±0.2	6.95	—	—	—	—
		6.9±0.4	6.7±0.4	6.5±0.3	6.7±0.3	6.95	7.15	...	—
		7.3	7.0	7.0	...	—	—	—	—
	Jul. 53	7.8±0.3	7.3±0.5	7.2±0.5	7.3±0.5	7.3±0.2	7.1±0.1	7.2	—
		8.3±0.2	8.0±0.3	7.9±0.1	7.9	—	—	—	—
	Jul. 55	7.9±0.2	7.4±0.2	7.3±0.1	7.3±0.1	7.40	7.42	7.43	—
		8.0±0.4	7.4±0.1	7.5	...	—	—	—	—

Call	Jul. 56	7.4±0.4	6.3±0.5	6.0±0.4	6.7±0.3	7.0±0.3	7.3±0.2	7.45	-
	Jun. 57	8.1±0.9	7.1±0.5	7.0±0.1	...	-	-	-	-
		7.3±0.1	6.8±0.2	6.6±0.2	6.6±0.2	6.8±0.3	7.1±0.1	7.15	-
	Sep. 57	7.7±0.2	7.3±0.1	7.2±0.1	7.3	-	-	-	-
		7.5±0.4	7.2±0.5	6.7±0.3	6.9±0.4	6.9±0.2	6.95	...	-
Loughborough	Jun. 58	8.5±0.4	8.3±0.2	8.20	8.22	-	-	...	-
		8.2±0.2	7.4±0.1	7.6±0.3	7.3±0.3	6.9±0.1	6.9	...	-
		8.5±0.3	8.5±0.4	8.5	...	-	-	-	-
	Jun. 59	7.7±0.2	7.6±0.1	7.6±0.2	7.6±0.2	7.4±0.2	7.55	7.48	-
		8.1	8.0±0.2	8.0	...	-	-	-	-
Bute	Jul. 53	8.7±0.3	8.1±0.2	7.5±0.1	...	-	-	-	-
	Aug. 53	9.3±0.2	8.4±0.3	7.9	8.0	-	-	-	-
	Jul. 55	8.5±0.3	7.6±0.2	7.7±0.1	7.9	-	-	-	-
	Jul. 56	7.5±0.2	6.8±0.4	6.0±0.1	5.8	-	-	-	-
	Jun. 57	8.2±0.1	7.1±0.1	6.4	6.3	-	-	-	-
	Sep. 57	8.6±0.2	8.3±0.3	6.9±0.2	...	-	-	-	-
	Jul. 53	9.9±0.3	9.1±0.1	8.2±0.2	8.1±0.1	-	-	-	-
	Jul. 55	9.1±0.1	8.6±0.2	7.8±0.4	7.7	-	-	-	-
	Jul. 56	8.6±0.1	7.8±0.3	7.6±0.4	7.3±0.1	-	-	-	-
	Jun. 57	8.5±0.2	8.0±0.4	7.2±0.4	6.6	-	-	-	-
	Sep. 57	9.5±0.3	9.1±0.5	8.6±0.9	6.7±0.1	-	-	-	-
	May 51	7.6±0.2	6.4±0.3	7.3±0.2	7.6±0.2	7.9±0.1	7.9±0.1	...	7.98
	Aug. 51	8.9±0.2	8.1±0.4	7.8±0.2	8.0	...	...	...	...
	Oct. 51	8.4±0.2	7.7±0.7	7.6±0.2	7.9	...	7.9±0.1	7.91	...
	Mar. 52	6.9±0.4	6.8±0.5	7.0±0.6	8.0±0.3	8.1±0.2	8.2±0.2	7.93	...
	May 52	7.8±0.5	6.6±0.3	7.4±0.3	8.2±0.1	8.2±0.2	...	8.2±0.2	...
	Aug. 52	8.5±0.2	8.1±0.2	7.4±0.5	8.1±0.1	8.15	8.20	...	8.09
	Mar. 53	7.5	7.4±0.4	7.6±0.4	8.4±0.2	8.6	8.64	8.65	8.68
	Jul. 53	9.5±0.3	8.4±0.5	7.8±0.4	8.4±0.1	8.4±0.1	8.5±0.1	8.6	8.66
	Aug. 53	9.0±0.2	8.3±0.5	8.0±0.3	8.30	...	8.52	...	8.66
	Jun. 54	8.0±0.7	7.6±1.1	7.9±0.4	8.4±0.2	8.6±0.1	...	...	...
	Jul. 55	9.4±0.2	8.4±0.2	8.4±0.1	8.4±0.1	8.4±0.1	8.44	8.46	8.48
	Jul. 56	8.3±0.1	7.8±0.1	7.8±0.3	8.0±0.2	8.20	8.22	8.25	8.29
	May 57	7.5±0.9	7.0±1.0	7.4±0.4	8.2±0.1	8.16	8.1±0.1	8.2±0.2	8.05
	Jul. 57	8.8±0.1	8.0±0.2	7.5±0.1	7.9±0.3	8.0±0.2	8.1±0.1	8.11	8.11
	Sep. 57	8.9±0.2	8.2±0.3	7.9±0.5	7.8±0.3	8.0±0.2	8.0±0.2	8.1±0.1	...
	Nov. 57	7.9±0.4	8.0±0.3	7.8±0.4	8.0±0.2	8.0±0.2	8.0±0.1	8.1±0.1	...

TABLE VII.—Continued

Inlet	Date	DEPTH (METRES)						(Notes)
		20	50	100	200	300	400	
Bute (Cont.)	Feb. 58	7.4±0.4	7.9±0.1	8.0±0.5	8.3±0.3	8.2±0.3	8.0±0.1	8.11
	Mar. 58	7.6±0.3	7.8±0.2	8.0±0.2	8.2±0.3	8.2±0.2	8.07	...
	May 58	7.7±0.3	8.2±0.5	8.2±0.4	8.2±0.3	8.2±0.2	8.08	...
	Jun. 58	9.3±0.3	7.9±0.3	8.3±0.1	8.3±0.1	8.2±0.1	8.06	8.06
	Jun. 59	8.9±0.9	7.7±0.2	8.5±0.2	8.6±0.3	8.6±0.3	8.4±0.1	8.19
	Jun. 60	9.6±0.3	8.2±0.7	8.3±0.2	8.6±0.1	8.8±0.1	8.8±0.1	8.6
Ramsay	Jun. 54	10.1	7.4	8.5	8.7	8.7	—	—
	Jun. 56	9.9	7.3	7.7	8.1	8.2	—	—
Toba	Aug. 51	9.5±0.1	8.1±0.1	7.9±0.1	8.0	...	8.0	...
	Mar. 53	7.2±0.1	7.6±0.1	8.0±0.1	8.3±0.1	8.54	8.70	8.8
	Jun. 54	9.8±0.5	8.4±0.1	8.6±0.1	8.6	8.6±0.1	...	...
	Jun. 55	11.2±0.3	8.6	8.6	8.5±0.1	8.4	7.8	7.8
	Jun. 56	9.6±0.8	7.7±0.2	8.0±0.2	7.9±0.2	8.0±0.2	8.14	8.16
	Sep. 57	8.8±0.6	8.1±0.5	7.9	7.9±0.2	7.9±0.3	7.85	...
	Feb. 58	7.5±0.1	8.1±0.1	8.0±0.2	8.2±0.2	8.2±0.2	8.0±0.1	...
	Mar. 58	7.6	7.9	8.0±0.2	8.2±0.2	8.2±0.2	8.1±0.1	...
	May 58	7.91	8.1±0.1	8.2±0.1	8.2±0.1	8.2±0.2	8.3±0.1	...
	Jun. 58	8.2±0.4	8.1	8.1±0.1	8.2±0.2	8.2±0.2	8.3±0.1	...
	May 51	7.9±0.3	7.8±0.1	8.1	8.04	...	7.94	—
	Aug. 51	11.3±0.9	8.2±0.2	8.0	8.00	...	...	—
	Mar. 53	7.3	7.6±0.1	8.0±0.1	8.4	8.6	8.7	—
	Jul. 53	10.1±0.3	8.5±0.1	8.2	8.5	8.4	...	—
Pendrell	Aug. 53	11.5±0.6	8.9±0.1	8.2±0.1	8.4	8.5	...	—
	Jun. 54	9.6±0.3	8.2	8.65	8.63	8.5	...	—
	Jun. 56	11.2±0.6	7.5±0.3	7.9±0.2	8.18	8.23	...	—
	Sep. 57	9.6±0.2	8.1±0.1	7.86	8.00	7.9	...	—
	May 52	8.1±0.2	8.0±0.3	8.0±0.5	8.4±0.2	8.4±0.1	8.47	8.5
	Jun. 54	9.3±1.0	8.5±0.4	8.6±0.1	8.6±0.2	87±0.1	...	...
	Jun. 56	8.7±0.3	7.6±0.2	7.8±0.6	8.3±0.2	8.5	8.47	8.48
Jervis	May 57	8.4±0.5	7.7±0.4	7.7±0.5	8.3±0.2	8.4±0.1	8.44	8.48

Jul. 57	7.9±0.5	8.2±0.4	7.7±0.2	8.3±0.2	8.44	8.45	8.45
Nov. 57	8.9±0.2	8.4±0.6	8.4±0.5	8.3±0.2	8.4±0.1	8.42	8.44
Feb. 58	7.6±0.4	8.15	8.4±0.2	8.4±0.2	8.4±0.1	8.39	8.42
May 58	8.5±0.4	8.2±0.1	8.25	8.4±0.2	8.40	8.41	...
Jun. 58	8.4±0.2	8.2	8.35	8.5±0.2	8.41	8.40	8.39
Jun. 59	9.9±0.4	8.6±0.1	8.8±0.1	8.7±0.2	8.7±0.2	8.6±0.1	8.75
Jun. 60	8.4±0.2	8.3±0.2	8.4±0.4	8.8±0.1	8.8±0.1	8.8±0.1	8.94
Pr. Louisa							
May 52	10.8	8.8	7.7	...	-	-	-
Jun. 60	10.7	8.7	7.7	7.7 at 176 m	-	-	-
Sechart							
Jul. 57	11.1±0.4	8.8±0.4	7.5±0.2	7.43	-	-	-
Howe							
Mar. 53	7.8±0.1	8.0±0.2	8.3±0.3	8.6	...	-	-
Jun. 57	8.3±0.7	8.0±0.4	7.5±0.2	7.45	...	-	-
Indian							
Jun. 53	10.3±0.3	8.4±0.4	7.9	...	-	-	-
Sep. 53	11.3±1.1	10.7±0.8	7.92	7.91	-	-	-
Win. 56	9.4±1.3	8.3±1.3	6.7±0.5	6.4±0.1	-	-	(9)
Sum. 56	11.0±0.1	9.8±1.0	6.6±0.1	6.3	-	-	-
Win. 57	8.5±2.0	8.3±1.8	7.0±0.6	6.5±0.2	-	-	-
Sum. 57	10.8±0.3	9.6±1.2	6.6±0.2	6.4	-	-	-
Win. 58	8.8±0.8	9.0±0.8	7.9±0.2	6.8±0.3	-	-	-
Sum. 58	11.9±0.9	10.2±1.2	7.9±0.1	7.2±0.2	-	-	-
Win. 59	9.3±1.2	8.8±1.3	8.2±0.6	7.7±0.1	-	-	-
Sum. 59	11.5±0.6	10.4±1.6	7.9±0.2	7.7±0.1	-	-	-

Notes:

(1) When the $\pm$ range including at least 75% of the values at a particular depth (75% range) was ± 0.02 C degree or less its value has been omitted and the mean temperature has been quoted to the nearest 0.01 C degree. When the 75% range was between 0.03 and 0.07 C degree its value has been omitted and the mean temperature quoted to the nearest 0.1 C degree. When the 75% range was 0.08 C degree or over, its value has been quoted to the nearest 0.1 C degree.

(2) Data collected by Canadian Hydrographic Service.

(3) Data collected by Pacific Oceanographic Group, Sta. Do 6, 8, 10 only.

(4) Station Ga 4-14.

(5) Stations Ga 1-3.

(6) Data collected by Pacific Oceanographic Group, Sta. Ga 4, 6 and 10 only.

(7) Station Sp 5 only.

(8) See Note (9), Table VI.

(9) See Note (11), Table VI.

entrance of saline water. The difference between the two is attributed to the larger runoff into Seymour (Table II).

It is also noted that in any region, inlets with shallow sills have deep water of lower salinity than at the same depth outside, but of higher salinity than at the sill depth outside. The water temperature however is sometimes higher and sometimes lower than outside. These facts may be related to the character of the circulation which is discussed later.

The salinity in the deep zone generally increases with depth. A few inversions have been noted in the deepest water where the salinity gradients are small but these are usually within the limits of error of salinity determination with the method in use.

3.22 TEMPERATURE MINIMUM

In contrast to the vertical salinity distribution which shows a continuous increase from surface to bottom, the temperature profiles often show maxima or minima at intermediate depths. In the spring and summer the surface water is the warmest in any vertical column and the temperature decreases as depth increases in the shallow zone except occasionally when wind mixing has created an isothermal layer, or where at the head of an inlet cold fresh water is overlying warmer saline water. Usually there is a thermocline closely associated with the halocline and below this in many of the inlets the temperature decreases to a minimum at 15 to 100 m depth. It then rises and becomes isothermal or nearly so in the deep water. Sometimes there is a temperature maximum at 40 to 200 m between the minimum and the isothermal deep layer. There are twelve inlets, mostly shorter ones, in which a temperature minimum has not been observed or is uncommon.

The temperature minimum appears most marked and is generally a feature in Bute. The minimum temperature is as much as 2 C degrees less than that of the deep isothermal water, but, as Fig. 19 shows, the extent of the minimum varies from year to year. During the extensive survey of 1951 a marked minimum was also observed in Seymour and Douglas. It was less conspicuous elsewhere (i.e. less than 1 degree) but was evident to some extent in most inlets. In 1956 and 1957 the minimum was very conspicuous in several of the large inlets (Jervis, Bute, Knight, Kingcome, Burke and Dean). On the other hand, in 1958 the minimum was much less conspicuous than usual in Jervis, Toba and Bute although more conspicuous in Knight.

Figure 19 shows that the minimum differs in appearance in different years and also indicates a change in appearance during a year (e.g. 1951, 1952, 1957, 1958). Figure 20 shows a series of vertical temperature profiles in Bute which illustrates in more detail the variation in appearance of the minimum during a period of 14 months.

This temperature minimum has been attributed (Pickard, 1953) to winter cooling of the upper part of the water column followed in spring and summer by warming from the surface. The temperature of the minimum, the difference

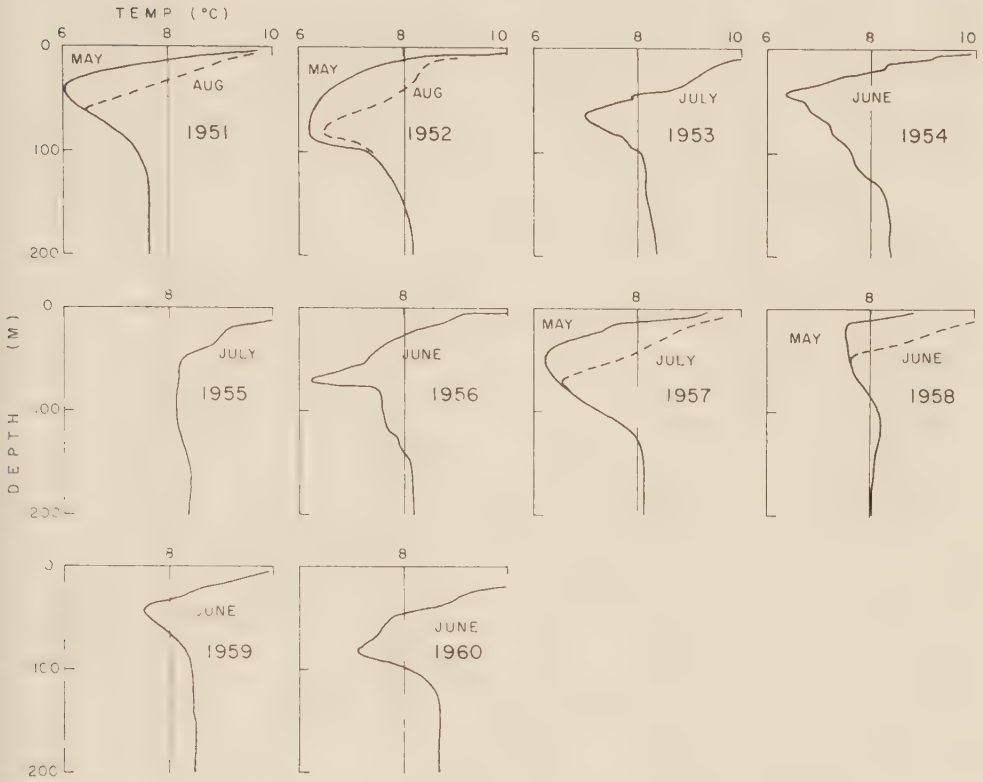


FIG. 19. Temperature minimum at Sta. 6, Bute Inlet, 1951-1960.

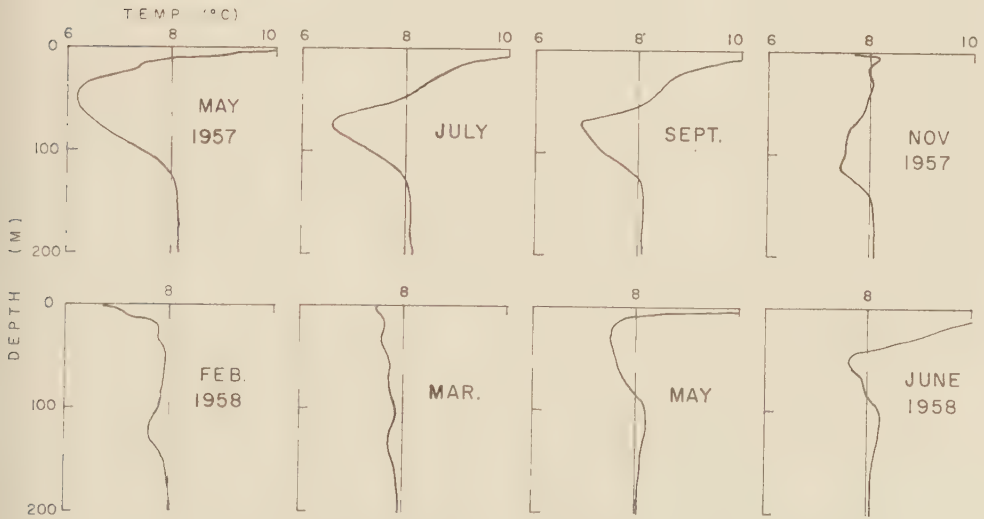


FIG. 20. Temperature minimum at Sta. 6, Bute Inlet from May 1957 to June 1958.

from that of the deep isothermal water, and possibly the depth of the top of the isothermal layer, must then be some indication of the amount of cooling in the previous winter or winters. Unfortunately there are no meteorological stations in the southern inlets and therefore there is no opportunity to correlate local climate directly with the temperature minimum. However, an examination of the temperature records at a selection of the coastal stations (Meteorological Division, 1950-1958) indicates that the climatic fluctuations at all of these follow essentially the same pattern, and it may be legitimate to use the temperature records for Vancouver Airport for comparison with the water temperatures in the southern inlets. For instance the temperature minimum was very marked in Bute in 1951 (Fig. 19) and the value was low (6.0°C) in May. In succeeding years the minimum became less marked and the temperature rose to 8.2°C in 1955. In 1956 the minimum was again very marked and the value had fallen to 6.4°C and in 1957 to 6.3°C . In 1958 it had risen to 7.6°C . For comparison the mean temperature at Vancouver Airport was lower than usual during 1949-50, was close to the long-term mean during 1951-54, below this mean in the winter of 1955-56, and above it again in 1957-58. The temperature minimum in the water therefore shows some inclination to follow the mean air temperature. More specifically there is an indication that below-normal air temperatures during January-March may be particularly effective in determining the extent of the minimum. This is the time of year when the stability of the water column in the upper 100 m is least because the salinities are highest (see Section 4.2). It is also the time when strong winds ("Squamishes") bring cold air down from the interior plateau to the inlets. These may be a significant factor in causing turbulent mixing and cooling of the water. It would be interesting to follow the development of the temperature minimum by closely spaced cruises during the winter, studying the heat budget at the same time. The best series obtained so far was in 1957-58 (Fig. 20) but unfortunately the winter was not a cold one and the minimum in 1958 was not conspicuous.

Mohn (1887) describes an apparently similar temperature minimum at 10 to 100 m depth in certain Norwegian fjords. Nordgaard (1903) also describes a marked temperature minimum in By Fjord and Hjelte Fjord. It is at the surface in the winter and descends subsequently to 20 to 50 m in April. In By Fjord the temperature is substantially constant from 80 m to the bottom at 150 m and in Hjelte Fjord from 120 m to the bottom.

3.3 PERIODIC CHANGES

3.31 SEASONAL CHANGES IN SALINITY AND TEMPERATURE

The character of the seasonal variation in salinity and temperature in Bute for 1950-52 was described by Tabata and Pickard (1957) and summarized by stating that an annual cycle of change was evident to a depth of 60 feet (about 20 m) in salinity but to about 150 feet (about 50 m) in temperature. Data from the series of eight cruises in 1957-58 are shown in Fig. 21 and 22 to supplement

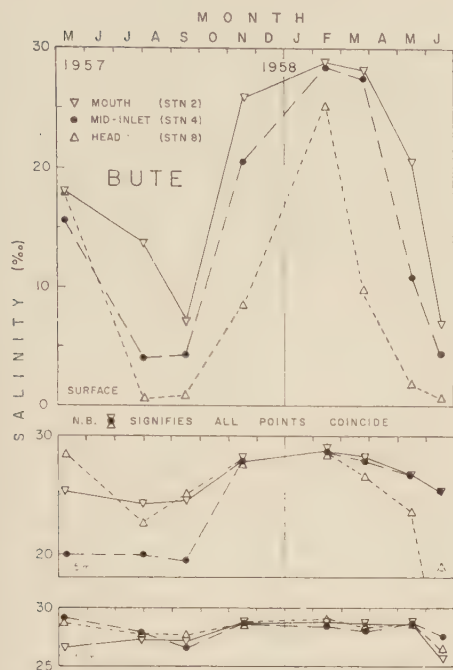


FIG. 21. Seasonal variation of salinity in Bute Inlet, 1957-1958.

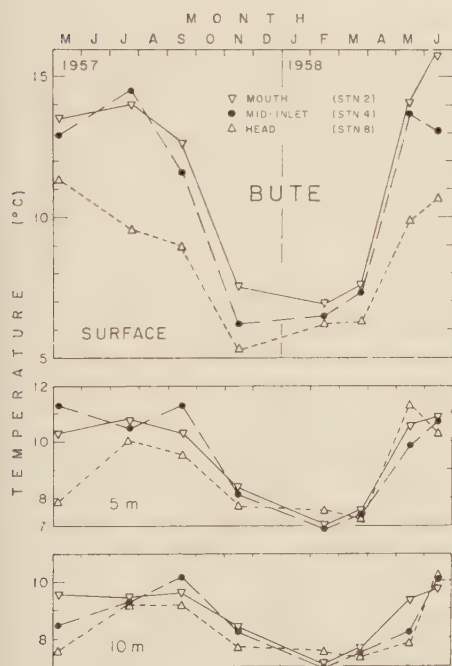


FIG. 22. Seasonal variation of temperature in Bute Inlet, 1957-1958.

those for 1950-52. The later series, together with data from successive winter and summer cruises at other times, suggests that the seasonal fluctuation in salinity may extend to 30 m, and that the seasonal temperature fluctuations may extend to 100 m particularly if the winter is unusually cold. (It should be noted that the salinity values for the cruise of September 1957 appear to be 0.15 to 0.25‰ low compared with neighbouring cruises while the temperature values show no significant difference. The accuracy of the salinity values is therefore questioned and the slight minima in salinity at 50 m and 75 m for September 1957 are not regarded as significant evidence of deeper penetration of the seasonal salinity fluctuations.)

The ranges of seasonal variations at the surface in Bute are from 6 C degrees and 25‰ at the inlet head to 10 C degrees and 22‰ at the inlet mouth. In the surface layer the temperature maximum occurs in July or August and the minimum in December or January, while at 50 m the maximum occurs in September and minimum in February or March.

The other inlet for which there are adequate data to determine the seasonal variations is Indian. Gilmartin (1960) has described a series of observations at approximately monthly intervals over a period of 3 years. In this inlet the seasonal variations of salinity are clearly evident to 50 m. There is some variation at 100 m but this is irregular and appears to be attributable to the occasional influx of water from outside rather than being a direct result of seasonal runoff variations. There is a seasonal temperature variation evident to 100 m. The ranges of seasonal variations at the surface in Indian are 12 to 17‰ in salinity and 10 to 17 C degrees in temperature.

The much larger runoff into Bute is taken to be the cause of the larger salinity variations than in Indian, while the low temperature of the runoff into Bute (from glaciers) limits the seasonal range of temperature in this inlet.

The only other inlet for which winter and summer observations are available is Jervis. The observations indicate that the variations in this inlet are similar to those in Bute which are taken to be typical of the situations in the larger inlets.

Nordgaard (1899) describes seasonal variations in some fjords as being observed to 200 m. This greater penetration may be a consequence of the lesser stability of the waters in the Norwegian fjords where the shallow water salinities are not as low as in the British Columbia inlets.

3.32 LONG-TERM CHANGES IN SALINITY AND TEMPERATURE

The seasonal variations in salinity and temperature in the shallow zone are so large that with the infrequent observations over most of the period of study it is not possible to detect any significant long-term variation. In the deep water the situation is the opposite and while no significant seasonal variation is apparent there is evidence of year-to-year changes. For instance, in Bute the temperature range in the water from 300 to 600 m depth is generally within 0.1 to 0.2 C degree along the length of the inlet at any one time, and long-term differences greater than this can be considered significant. It will be seen from Table VII that

there was an increase in temperature of 0.6 to 0.7 C degree from 1951 to 1953 and then a decrease of about the same amount to a minimum in 1957 with a subsequent rise. The salinity showed a small rise in 1953, a decrease until 1956, a rise in 1957, a decrease in 1959, and then a small rise in 1960. These data for Bute are illustrated in Fig. 23. The data plotted are taken from Tables VI and VII and are the average values along the length of the inlet at each depth below the level of seasonal change. The scales for temperature and for salinity have been selected so that a displacement of the temperature line from the mean by

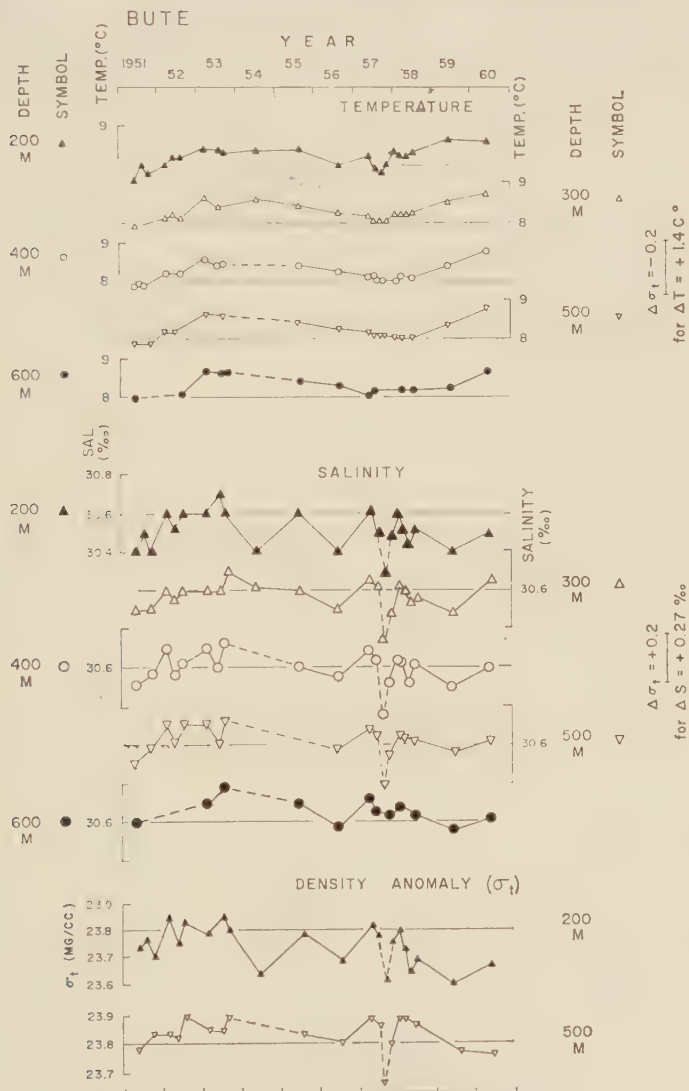


FIG. 23. Values of salinity, temperature and density anomaly of the deep water in Bute Inlet, 1951-1960.

a given distance (say 1 cm) represents the same change in σ_t as does the same displacement of the salinity line. This facilitates the comparison of the significance of fluctuations of these two quantities which are themselves independent and of different physical character but which together determine the density of sea water. This in turn determines the depth at which a particular water mass will find itself in static equilibrium. The graphs of σ_t for depths of 200 and 500 m at the bottom of Fig. 23 are again plotted to the same scale to show that the salinity is the main determining factor in density even in the deep water of this inlet. When reading Fig. 23 it should be noted that in terms of the effect on density the precision of the temperature points (estimated at about ± 0.1 C degree including the experimental error and the averaging of several points along the inlet length) is considerably greater than that of the salinity points (estimated at ± 0.05 to 0.1%).

In Fig. 23 there is some indication of the rise in temperature occurring more abruptly at 600 meters than at the lesser depths. The number of observations are too few to warrant stressing this point, particularly as the change in salinity appears to occur much less abruptly. However, since both the temperature and salinity generally increase slightly with depth in the deep water it is clear that an

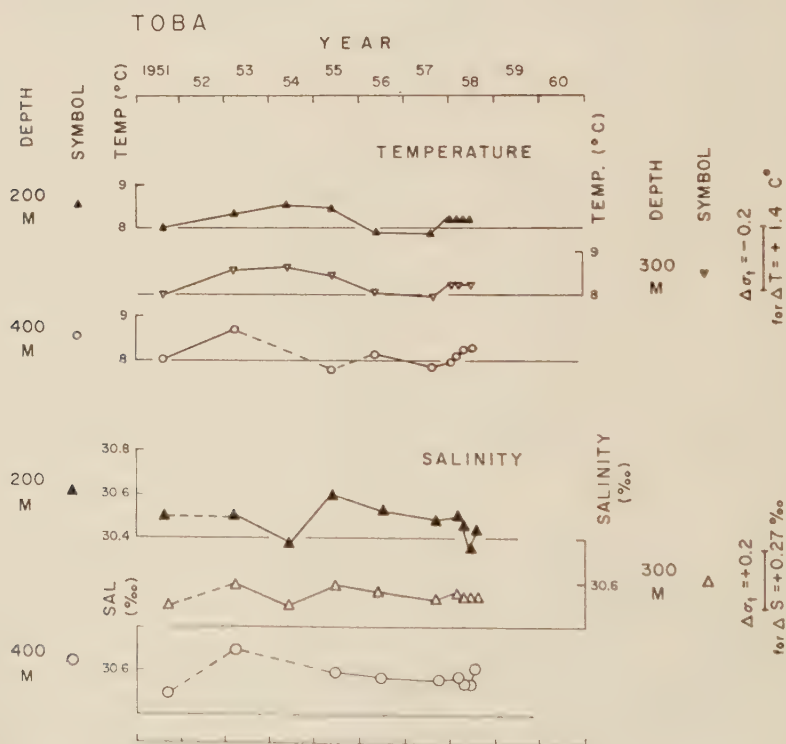


FIG. 24. Values of salinity and temperature of the deep water in Toba Inlet, 1951-1958.

increase in either cannot be explained by downward diffusion and it is concluded that the increases in the 1951 and 1959 periods must be due to an inflow of deep water from outside the inlet. The slow decrease in temperature and salinity after 1953 could be explained by diffusion upward with an eddy diffusion coefficient of the order of $0.02 \text{ cm}^2 \text{ sec}^{-1}$. This may be compared with the values of 0.2 to $1.2 \text{ cm}^2 \text{ sec}^{-1}$ estimated for depths of 90 to 130 m just below the temperature minimum (Tabata and Pickard, 1957) where the gradients of temperature and salinity are greater.

The amount of data available for other inlets is less than for Bute. Toba (Fig. 24) shows essentially the same pattern as Bute at 300 and 400 m from 1951 to 1958. Jervis (Fig. 25) shows a smaller rise in temperature at 300 m, 0.4 C

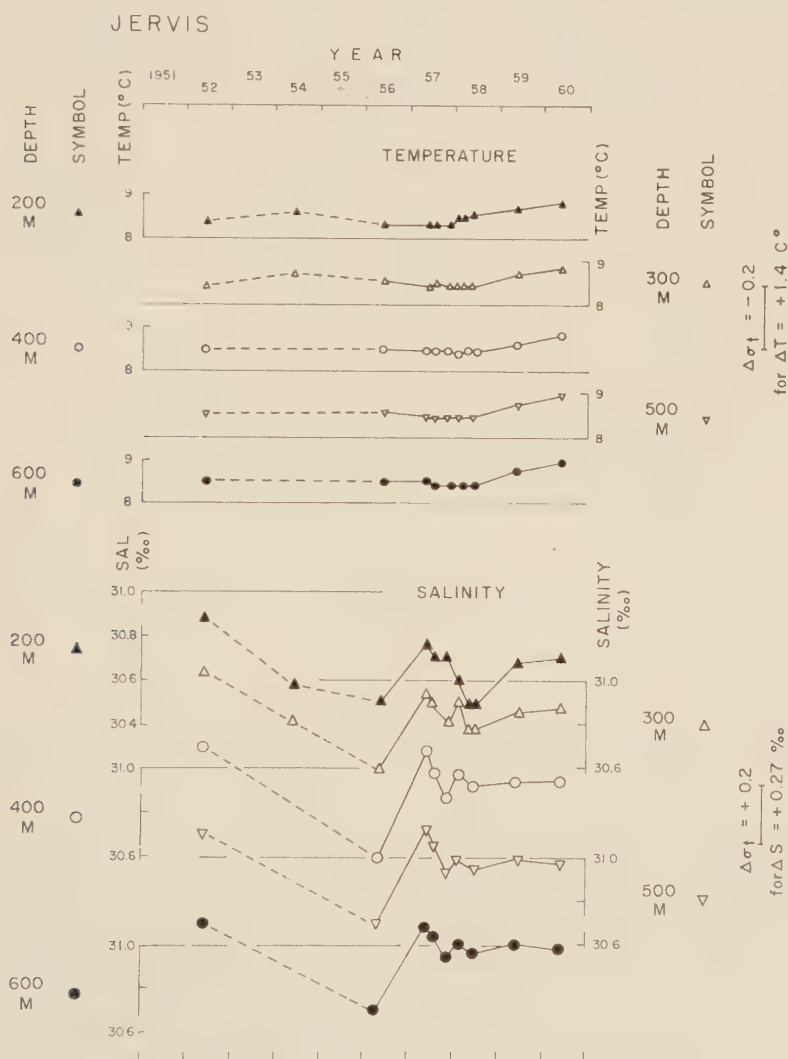


FIG. 25. Values of the salinity and temperature of the deep water in Jervis Inlet, 1952-1960.

For the inlets further north there are only a few scattered observations which are summarized in Table VIII in terms of the change from the earlier year quoted to the later, while the observations of Thompson and Barkey (1938) are given in Table IX with the present author's observations in 1951 for comparison.

TABLE VIII. Changes of temperature and salinity of deeper waters in some northern inlets between the years stated.

Inlet	Years	Depth range	Change of:	
			Temperature	Salinity
		<i>m</i>	C°	‰
Douglas	1951 to 1954	100-400	+0.5	-0.1
Gardner	1951 to 1954	100-300	+0.6	-0.1
Dean	1951 to 1956	100-300	-0.1	-0.1
		400-500	nil	nil
Burke	1951 to 1956	100-300	-0.1	-0.2
		300-500	+0.2	nil
Rivers	1951 to 1956	100-300	-0.2	nil
Moses	1951 to 1956	200	+0.7	+0.2
Kingcome	1953 to 1955	100	nil	+0.3
		200-300	nil	nil
Kingcome	1955 to 1957	100-200	-0.5	-0.3
		300	nil	+0.1

TABLE IX. Temperature and salinity in Seymour Inlet in 1937-38 and in 1951. (Data for 1937 and 1938 from Thompson and Barkey, 1938.)

	September 1937	March 1938	June 1951
Temperature (°C):			
Surface	14.73-16.04	6.83-7.19	9.5-15.8
75 m	7.87-8.49	7.06-7.95	7.1-8.3
550 m	7.02	7.19	7.35
600 m	7.15	7.47	...
Salinity (‰):			
Surface	5.5-12.7	25.3	1-23
Deep	28.95-29.02	...	29.02-29.06

It is concluded from the evidence available that there is no annual cycle of change of properties below 100 m but that changes do take place irregularly at intervals of a year or more. The question remains as to whether these changes represent changes in the properties of basically static water masses or are evidence of replacement of significant proportions of the deep-water masses from outside. The latter process is believed to be the more probable and in any event is the only means whereby an *increase* in salinity of the deep water can occur.

4. DENSITY

4.1 DENSITY DISTRIBUTION IN SHALLOW AND DEEP ZONES

In the shallow zone and to about 50 m the density of the water is determined almost entirely by the salinity, particularly in the Group A inlets, and there is no point in describing the density distribution separately. However, in the deep water the effect of temperature is not insignificant and the density distribution which includes the effect of both salinity and temperature shows some features which should be mentioned.

A plot (not given) of the density at a selection of depths from 20 to 500 m against the latitude of the approximate middle of the inlet length suggests that very broadly the inlets might be divided into two groups. The northern inlets from Portland to Smith, with some exceptions, have much the same density at the same respective depths. For the remaining inlets the density at any depth tends to decrease to the southward. Looking more closely one can pick out basic groups of northern and southern inlets, similar to those selected on the basis of temperature and salinity, also an intermediate group. The mean values of σ_t are given in Table X, and also shown graphically in Fig. 27. There are exceptions from the main groups and these are included in the Table for subsequent comment. The intermediate inlets are given individually, since the change of mean values from one to another, in relation to the variation in any one of them, is such that grouping them together would obscure certain features on which it is desired to comment.

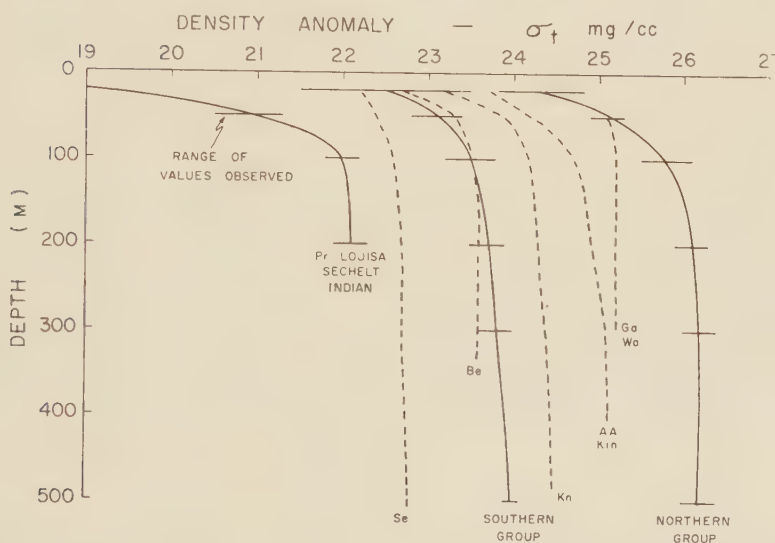
The broad feature of greater density in the northern than in the southern group is attributed to their more direct connection with the Pacific Ocean as the ultimate source of the densest water along the coast. The lesser density in the southern group is attributed to the fact that these open into the Strait of Georgia where the water is of lesser density than in the Pacific. It will be noted that the difference in σ_t between the southern and the northern groups is very significant (about 2.2 mg/cc).

The southern inlets which depart from the main group (Sechelt, Princess Louisa and Indian) are those which have a restricted entrance and it is assumed that it is this feature which holds the lower-density surface water in these inlets. At the same time it should be noted that it is not only the surface but also the deeper water which is of lesser density by 1 to 2 mg/cc within the inlets than outside. Of the northern inlets, only Alice, Work and Draney have comparatively narrow entrances and these all have water of lesser density than other inlets in their region. The low values in Gardner are attributed to its shallow sill.

Among the intermediate group, Seymour and Belize have restricted entrances and again show lesser densities than others in the region. Although these two inlets have a common entrance there is a significant difference between their waters at all depths listed, that in Seymour being less dense by 0.6 to 0.9 mg/cc

TABLE X. Mean values of σ_t for British Columbia mainland inlet waters.

Inlets	Depth (metres)					
	20	50	100	200	300	500
Northern group:						
Portland C. to Smith	24.3	25.1	25.8	26.1	26.2	26.2
Exceptions:						
Alice and Observatory	23.5	24.5	24.6	24.8	25.0	—
Work, Gardner (Sta. 8 to head)	...	...	25.2	25.2	25.2	—
Draney	22.8	23.5	24.3	—	—	—
Intermediate group:						
Belize	22.7	23.3	23.5	23.6	23.6	—
Seymour	22.2	22.4	22.6	22.7	22.7	22.8
Kingcome	23.7	24.2	24.7	24.9	25.1	—
Knight, Call	23.2	23.9	24.2	24.3	24.4	24.5
Southern group:						
Bute to Howe	22.5	23.1	23.5	23.7	23.8	24.0
Exceptions:						
Princess Louisa, Sechelt, Indian	18.9	20.9	22.0	22.1	—	—

FIG. 27. Mean vertical profiles of σ_t in British Columbia mainland inlets.

than that in Belize. According to the best information available (Trites, 1955) the former inlet has more fresh water runoff than the latter and this is taken to be the reason for the difference in densities through the difference in salinities. Since the deep water as well as the shallow has a lesser density in Seymour it must be deduced that despite the conclusion (Tully, 1949, p. 10) that the chief mixing process in these estuaries is that of more saline deep water *upward* into the less

saline upper layer, yet there must be some downward diffusion of fresh water sufficient to maintain the observed difference between the two inlets which differ essentially only in fresh water supply. Even in low-runoff inlets, as long as the entrance is restricted the water is less saline than outside.

Generally the difference in σ_t between the 100-m level and the deepest water in any inlet is less than 0.5 mg/cc. In some inlets with shallow sills the difference in density between the sill depth and the deepest water is smaller than this, e.g. Observatory, Work, Gardner inside Sta. 8, Belize and Seymour; but in other cases this is not so, e.g. Alice, Draney. The reason for near homogeneity of the water below sill depth in one group but not in the other is not known, no feature which might suggest a reason common to one group but not to the other having been recognized. It is pointed out that the above statement is based on only one survey of some of the inlets mentioned and it might be suggested that the distinction observed between the two groups may not be a permanent feature. However, for the inlets for which more than one survey has been made it appears that although there may be long-term variations in the values of the temperature and salinity that determine the density, the character of the vertical distribution does not change radically. It is therefore assumed for the present that homogeneity or otherwise of the water below sill depth is a feature which requires explanation.

4.2 STABILITY

In the previous section it has been shown that the large changes of salinity and temperature with depth, particularly those of salinity, give rise to large changes in density with depth (Fig. 27). Hesselberg and Sverdrup (1915) showed that the vertical gradient of density determines the magnitude of the Archimedean restoring force on a water mass displaced from its natural depth. This in turn determines the amount of energy needed for the displacement of a water mass as the first step in a mixing process between different levels. Hesselberg (1918) introduced the term "stability" defined as:

$$E = \frac{1}{\rho} \times \frac{d\rho}{dz}$$

as a measure of the unwillingness of a water mass to undertake vertical motion. For the depths (z) of only a few hundred metres in the inlets the pressure effects on density (ρ) are small and the stability may be approximated by:

$$E = \frac{1}{\rho} \times \frac{d\sigma_t}{dz} \times 10^{-3}.$$

Using units of grams per cubic centimetre (g/cc) for density, milligrams per cubic centimetre (mg/cc) for σ_t , and metres for depth, the units of E are metres⁻¹. The numerical values of E found in nature range from high values of the order of 10^{-2} to low values of 10^{-8} which approach the limit of experimental error.

As the stability of the water column exerts an influence on the rate of vertical mixing, and also determines the period of internal waves, it may be regarded as a significant characteristic of the inlet waters. Values of the stability have been calculated for a number of inlets. Typically the highest values are found in the upper 10 m, and seasonal variations occur in the upper 20 m as a consequence chiefly of the seasonal variations of salinity. The range of values observed in a large-runoff inlet is indicated for Bute in Fig. 28 where stability is plotted on a logarithmic scale as $\log_{10} E$ against depth. The depth scale has been magnified between 100 and 20 m and further between 20 m and the surface to show in more detail the regions where the greatest values and variations occur. The values shown are for four cruises during the summer period of large runoff in 1957 and 1958 and a smooth line has been drawn through them. The dashed line shows the smoothed line drawn through values calculated for the winter period of 1957-58 for comparison. The highest values of $E = 10^{-3}$ to 10^{-2} m^{-1} occur in the halocline. Figure 30 compares in more detail the distribution of temperature, salinity and stability in the upper 20 m near the head of Bute.

It may be noted for comparison that values of stability in the coastal waters outside the inlets are of the order of 10^{-5} while values typical for open ocean areas are from 10^{-5} to 10^{-8} m^{-1} . The values in the surface layers of the large-runoff inlets are therefore 100 to 1000 times as great as open ocean values in the upper layers.

The seasonal variations below 50 m are not significant. It is pointed out that in the deeper water where the stability is least the accuracy of determination of E becomes small, being determined chiefly by the probable error in the determination of salinity. If it is assumed that individual salinity determinations are accurate to $\pm 0.02\text{‰}$ this puts a limit of approximately $\pm 30 \times 10^{-8} \text{ m}^{-1}$ on the calculated values of stability where the observed depth interval is 100 m.

It should be noted that the values of stability have been calculated from the values of density at observed depths. Except for special cases, such as those described by Fig. 30, the observations available are usually not more closely spaced than 2 m. Calculation of the stability from such data will give minimum values and there are indications that the gradient of the pycnocline is often greater than obtained by linear interpolation between observed depths. The highest value of stability recorded in the British Columbia inlets is $1.1 \times 10^{-2} \text{ m}^{-1}$ but it is possible that values as high as $2 \times 10^{-2} \text{ m}^{-1}$ occur.

It is seen from Fig. 28 that the seasonal variations in Bute are chiefly in the upper 10 to 20 m and it is apparent that in the winter the stability at Sta. 8, near the inlet head, does not decrease as much as elsewhere. The probable explanation is that the smaller runoff in the winter is the prime cause of the smaller stability and that a secondary cause is the mixing due to the stronger winds which occur in winter than summer. These effect greater mixing in the upper

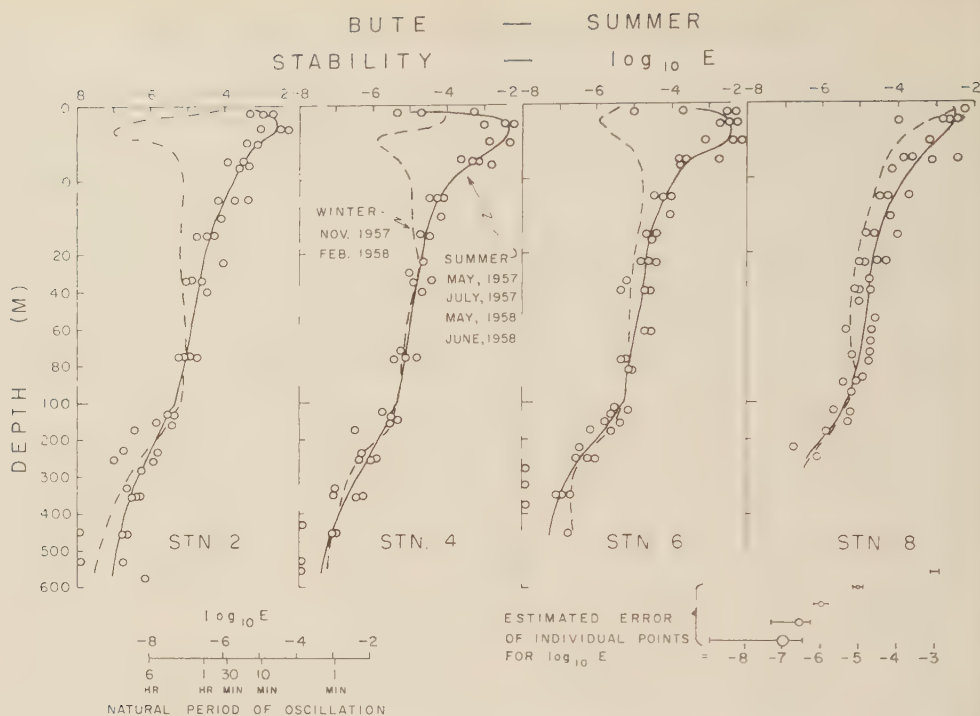


FIG. 28. Vertical profiles of the stability of the water at some stations in Bute Inlet, summer and winter.

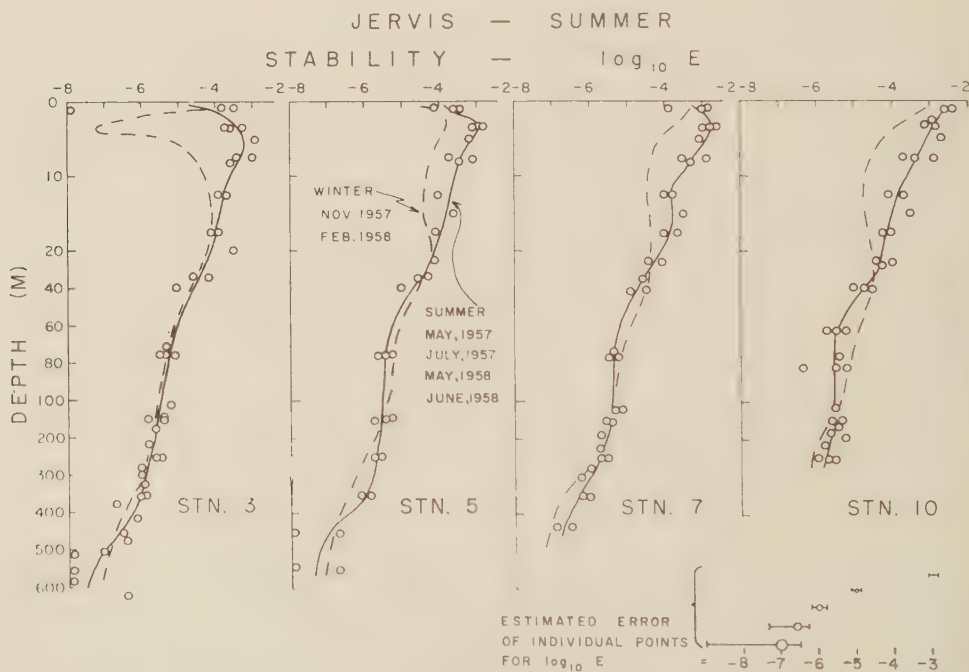


FIG. 29. Vertical profiles of the stability of the water at some stations in Jervis Inlet, summer and winter.

20 m particularly away from the stabilizing effect of the fresh water entering at the inlet head.

Figure 29 shows stability data for Jervis, a deep inlet with a smaller runoff than Bute. The difference in stability between winter and summer in the upper 10 m is less than in Bute but below 50 m there is no significant difference in the stability of the water in the two inlets.

On examining the values for stability in other inlets it is found that there is little difference between high- and low-runoff inlets below the surface layer of depth 20 to 30 m directly influenced by runoff. Values in some of the inlets with

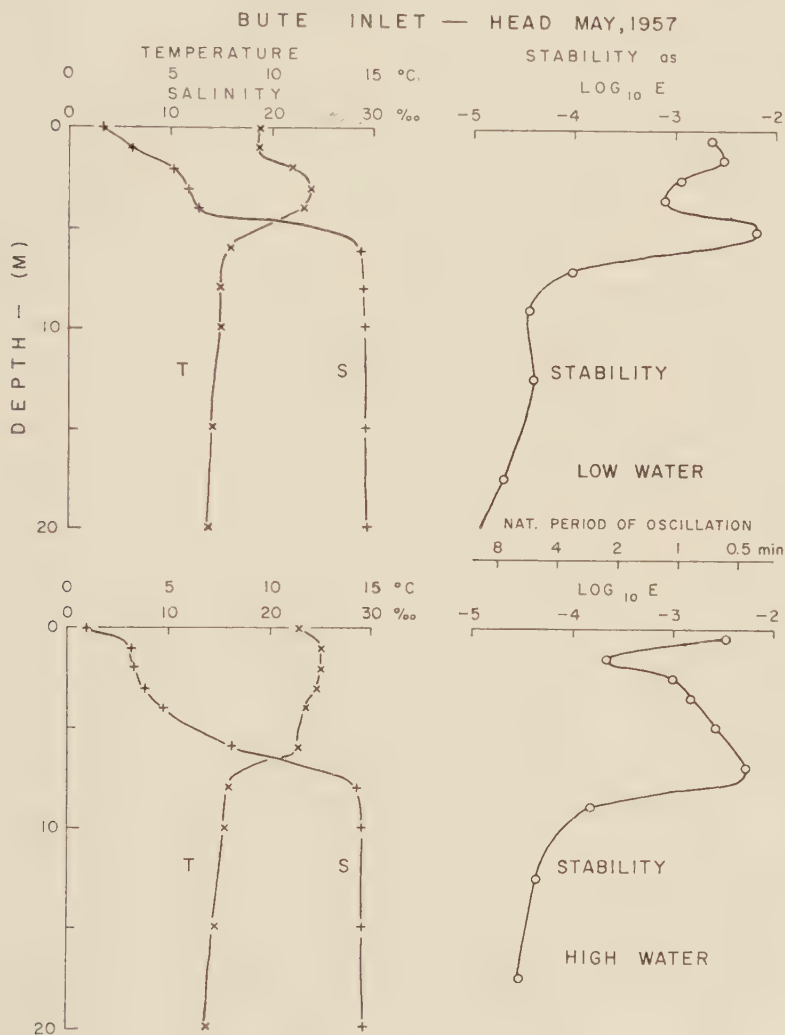


FIG. 30. Vertical profiles of salinity, temperature and stability at closely spaced intervals at the head of Bute Inlet.

deep basins such as Matheison-Kynoch are less than in Bute by a factor of 2 to 4 between 100 and 300 m but at greater depths the stability values in all the inlets are between $30 \times 10^{-8} \text{ m}^{-1}$ and zero, i.e. not significantly different.

It can be shown that the period of vertical oscillation of a displaced water mass is determined chiefly by the stability of the water for moderate depths (Eckart, 1960). A few representative values for the period corresponding to different values of stability are shown in Fig. 28 for reference. In the surface layer the period is of the order of minutes, increasing to an hour or more in the deep water.

5. DISSOLVED OXYGEN

5.1 MAIN FEATURES

It is much less easy to generalize on the distribution of dissolved oxygen in the inlet waters than on the salinity or temperature. In the surface layer, values are usually at or above saturation, while in the deeper water they are below saturation. Maxima and minima in the vertical direction are common but do not follow a regular pattern. One of the few broad statements that can be made is that very low values (e.g. below 2 ml/l) are uncommon, and no zero values have been observed in the mainland inlets during the studies now being reported except occasionally in water in contact with the bottom in small-runoff inlets. (Very low and zero values for dissolved oxygen have been recorded in Saanich Inlet on the east coast of Vancouver Island, e.g. Carter (1934); I.O.U.B.C. Data Reports No. 4 and 5 (1955); Herlinveaux (1962, in press).)

It does appear, however, that the large-runoff inlets show smaller ranges of dissolved oxygen content along their length and with depth, than do the small-runoff inlets. Some of the oxygen data are summarized in Fig. 31, 32, 33 and 34 for the surface and for a series of depths to 500 m. In these Figures the oxygen content is presented against relative position in the inlet, i.e. all inlets have been normalized to the same length with the head at the right and the mouth at the left. In considering the oxygen data, graphs of oxygen content against relative position along the inlet were first plotted for each depth. In contrast to similar salinity and temperature plots the oxygen plots do not show any particularly consistent patterns which themselves suggest groupings of inlets. The oxygen content curves vary considerably from inlet to inlet and from cruise to cruise. As it is not practicable to present all the individual curves, the Figures simply show shaded areas within which the curves for the particular classification lie. The combinations of inlets here presented are based on the fresh water runoff characteristics of the inlets. They do show some similarities and contrasts but it is quite possible that some other significant grouping may exist at present unrecognized.

The data for the surface layer must be regarded as less reliable than the remainder as there are fewer actual surface observations and some of the values were obtained by extrapolation from subsurface values.

The large-runoff inlets included in Fig. 31(a) are Portland, Douglas, Gardner, Dean, Burke, Rivers, Knight, Bute and Toba. Figure 32(a) includes the same group except for Knight which appears to be anomalous at the greater depths. The small-runoff inlets included in Fig. 31(b) are Observatory, Work, Surf, Laredo, Mussel, Kynoch, Spiller, Roscoe, Draney, Smith, Belize, Seymour, Loughborough, Jervis and Sechelt. Fig. 32(b) includes the same group except for Belize and Seymour. The curves for these two inlets are shown separately in Fig. 31(c) and 32(c) for subsequent comment. Figures 33(a) and 34(a) show the values for all cruises on record in Bute, Fig. 33(b) and 34(b) for all in Knight, and Fig. 33(c) and 34(c) for all in Jervis.

In the shallow zone from the surface to 20 m, while there is in most cases a somewhat larger range of values in the small-runoff inlets as a group than in those with large runoff, the differences are not very marked. The difference is more marked between individual inlets such as Bute and Jervis (Fig. 33(a) and (c)).

At depths of 50 m and more there is a more consistent difference between the large- and small-runoff inlets as groups, the latter showing a greater range of values (e.g. Fig. 32). The spread of the shaded area toward the inlet head in the plots for these small-runoff inlets is chiefly because in some the oxygen content decreases toward the head whereas in others it increases. This behaviour is less evident in the large-runoff inlets. Seymour and Belize are shown separately in Fig. 31(c) and 32(c) to emphasize the difference between these neighbouring inlets which have a common outlet to the sea. Seymour would fall essentially into the small-runoff category. Belize is definitely a small-runoff inlet but appears to be extreme in oxygen distribution. The situation in these two inlets will be discussed later.

Of the remaining inlets, whose oxygen content distributions are shown in Fig. 32, Bute falls into the large-runoff group as might be expected. It is shown separately in Fig. 33(a) and 34(a) because so many more data are available (13 cruises from 1951 to 1959) than for the others listed in the large-runoff category (one or two cruises). Knight (seven cruises from 1952 to 1959, Fig. 33(b) and 34(b)) is certainly a large-runoff inlet but the oxygen values in it depart markedly from those in the remainder of this group, showing both a wider range at the lesser depths and generally larger values at the greater depths. Jervis, although physically a long and deep inlet, has a small runoff and its oxygen values fall within the areas on the plots in Fig. 31(b) and 32(b) for small-runoff inlets. It is shown separately in Fig. 33(c) and 34(c) to indicate two of the characteristics of this group, the marked change from head to mouth at the lesser depths and the consistency of the values, particularly at 200 m and below, from eight cruises from 1952 to 1959.

There is no evident geographical variation of oxygen values.



FIG. 31. Ranges of dissolved oxygen values at depths of 0 to 20 m along the length of large- and small-runoff inlets and of Seymour and Belize Inlets.

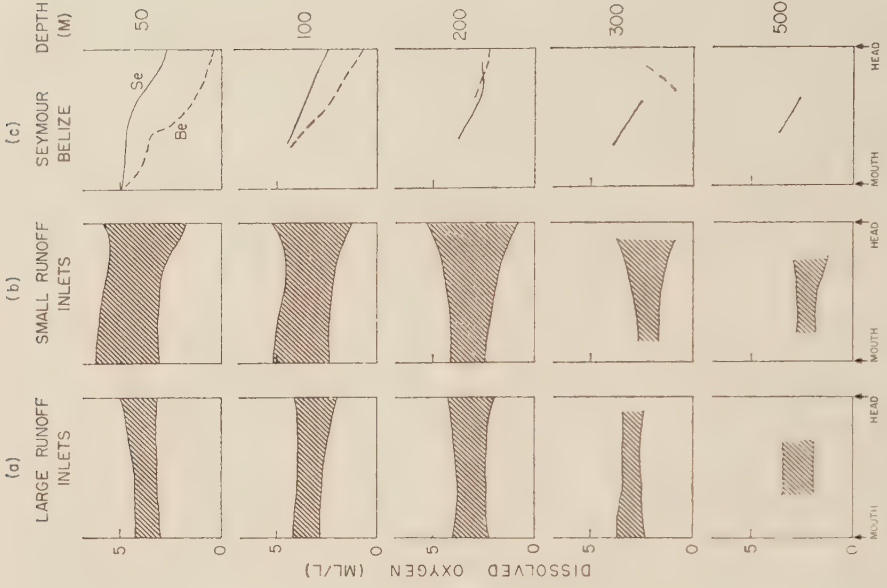


FIG. 32. Ranges of dissolved oxygen values at depths of 50 to 500 m along the length of large- and small-runoff inlets and of Seymour and Belize Inlets.

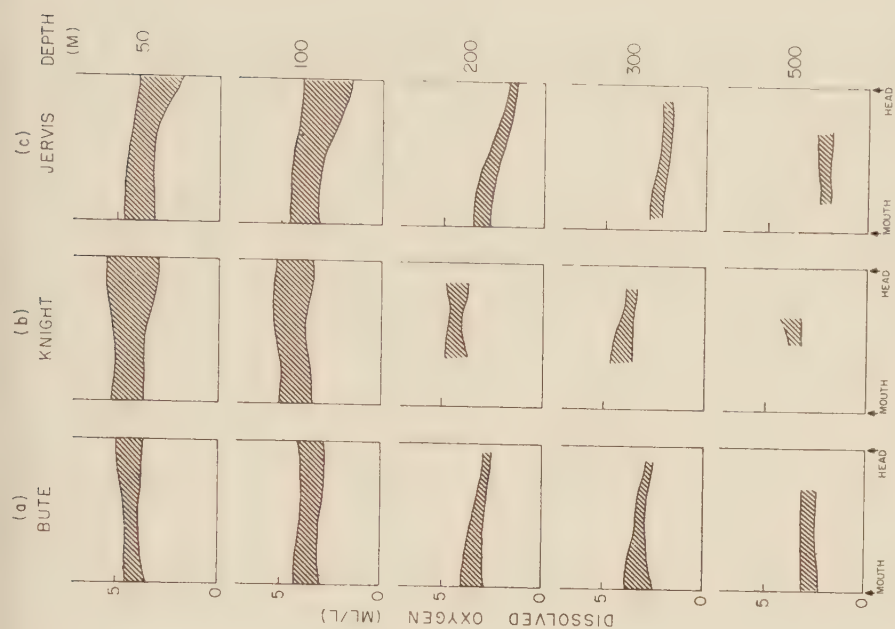


FIG. 34. Ranges of dissolved oxygen values at depths of 50 to 500 m for all cruises, 1951-60, in Bute, Knight and Jervis Inlets.

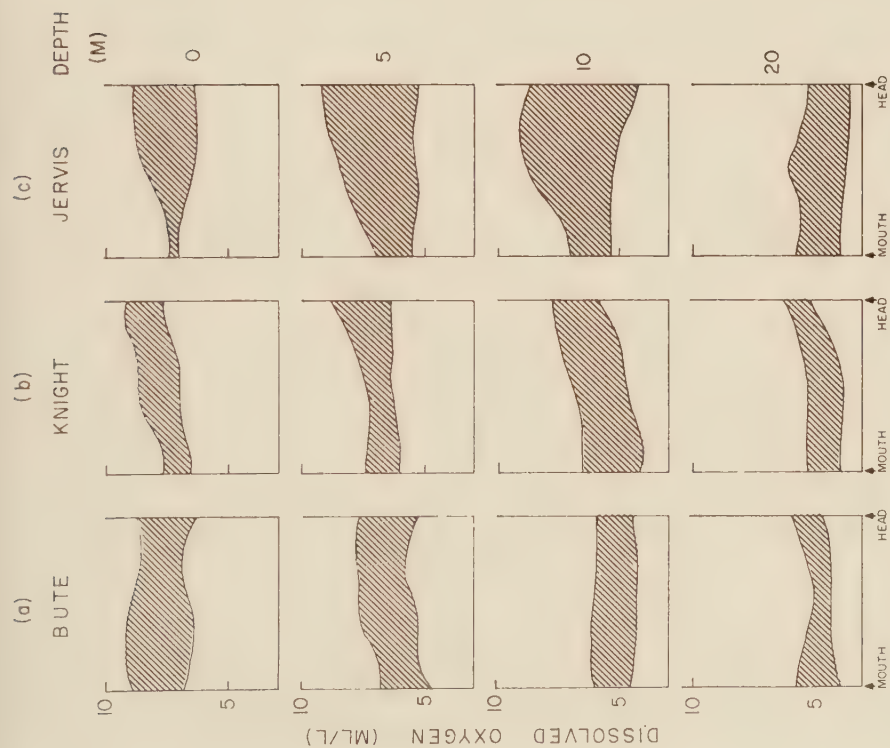


FIG. 33. Ranges of dissolved oxygen values at depths of 0 to 20 m for all cruises, 1951-60, in Bute Knight and Jervis Inlets.

5.2 OXYGEN MAXIMA

It was mentioned above that when the dissolved oxygen content of the water is plotted against depth at individual stations, maximum and/or minimum values are frequently observed in the vertical distribution. The existence of either a maximum or a minimum automatically implies the existence of one or more of the other and it is sometimes difficult to say which is the more significant. However, when one examines a considerable number of profiles for a particular inlet or type of inlet, these features may sometimes be present, sometimes absent, and therefore require description and, if possible, explanation.

Before continuing with the description of the oxygen distribution it will be well to define the term "saturation" or "saturation value" which will be used frequently. In this paper the term "saturation value" for dissolved oxygen is used to refer to the amount of oxygen which sea water is capable of holding in solution at the temperature and salinity of the water and at a pressure of one atmosphere, not at the *in situ* pressure. That is, it is implied that the normal source of dissolved oxygen is the atmosphere and that the oxygen dissolved in water at the surface will be in equilibrium with the atmosphere. Variations of actual barometric pressure from 76 cm of mercury are ignored. The nomogram of Tully (1949) based on the data of Whipple and Whipple was used to determine the solubility. The errors in the Whipple and Whipple data pointed out by Richards and Corwin (1956) are noted but are not significant in the present discussion. The oxygen content for saturation is markedly dependent upon the salinity and temperature of the water, decreasing as these two quantities increase. In the saline water below the halocline the saturation value is about 7 ml/l and in the less saline surface water it is up to 8 ml/l. In the plots of Fig. 35 and 36 which demonstrate some features to be discussed later, saturation values appropriate to the temperature and salinity of the surface water and to the temperature and salinity at 40 m depth are shown by arrows and the letter S. It should be noted that the saturation value generally increases slightly with depth in the low-salinity surface layer due to decrease in temperature and then in the halocline region drops by about 10% to the deeper value due to the rise in salinity.

Water which is homogeneous with respect to dissolved oxygen content over the full depth is never found in the inlets, though it may be found in some of the turbulent outside passages. The oxygen content is generally greatest at or near the surface and diminishes as depth increases. A single oxygen maximum at the surface is found either near the head of the large-runoff inlets or near the mouth (e.g. Fig. 9). In the former case, the value is very close to saturation for the temperature and salinity of the water, the salinity in these situations usually being small. This water is mainly river water, and as most of the rivers entering the inlets are turbulent it is assumed that the water attains its saturation value by solution from the atmosphere. On the other hand, maxima occurring near the mouth of an inlet usually have values greater than the saturation value and these are attributed to the oxygen production by phytoplankton which are usually present in these regions in the summer. Under these circumstances, an oxygen content of 110 to 130% of saturation is quite common (values up to 215%

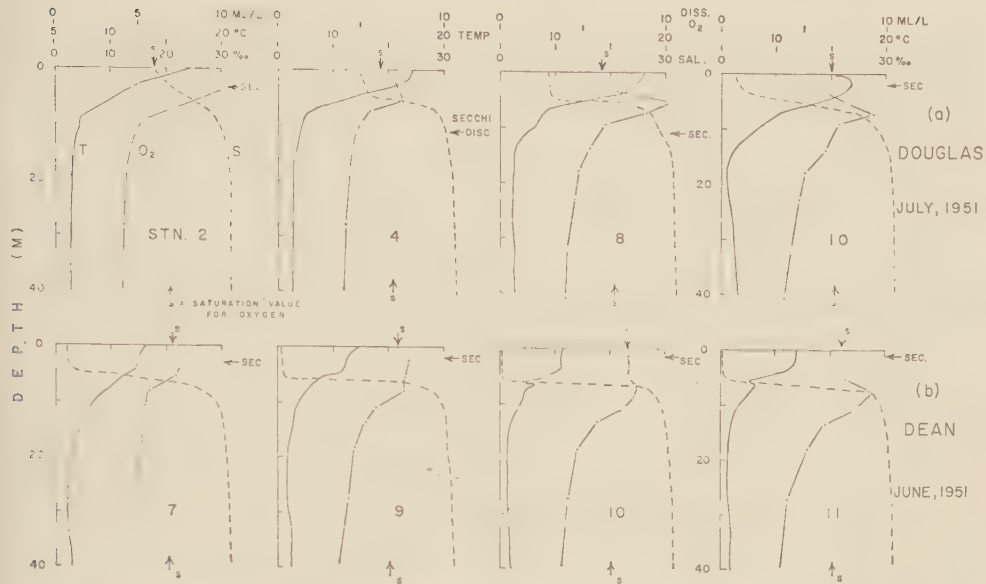


FIG. 35. Vertical profiles of salinity, temperature and dissolved oxygen in the upper 40 m in Douglas and Dean Channels.

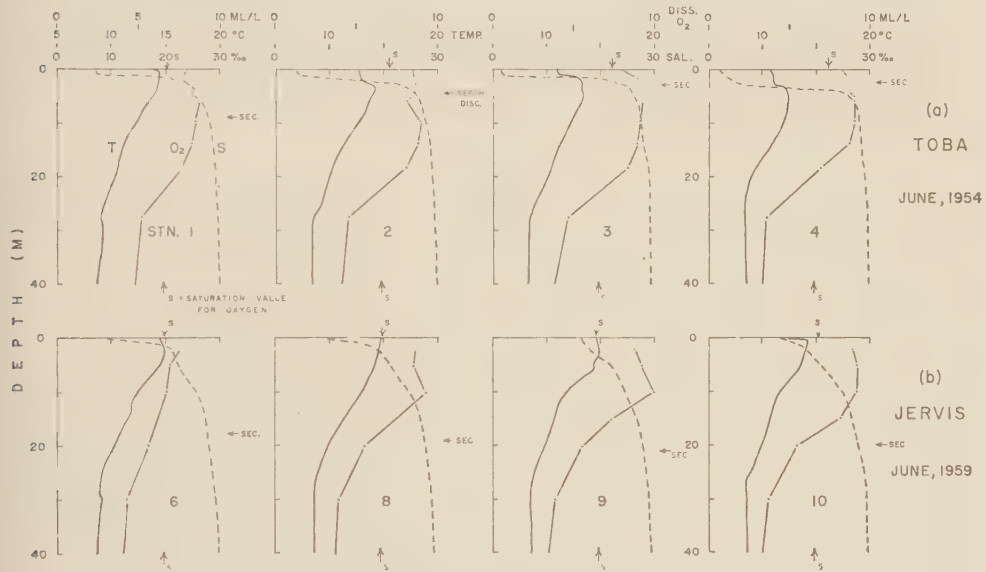


FIG. 36. Vertical profiles of salinity, temperature and dissolved oxygen in the upper 40 m in Toba and Jervis Inlets.

of saturation have been recorded in Saanich Inlet, I.O.U.B.C. Data Report No. 5). The actual value when highly supersaturated is not regarded as very significant, since experiments by the author have shown that it may be appreciably affected by the handling of the water sample. For instance, if a sample of such supersaturated water is shaken for about 15 seconds, the content may

decrease by several milliliters per liter. In standard sampling procedures such violent physical treatment is avoided, but it would not be surprising if the action of drawing samples into B.O.D. bottles might not cause some variation from the *in situ* value if the oxygen in its supersaturated state is so unstable.

Alternatively to a maximum at the surface, a maximum is common at 3 to 8 m depth and occasionally as deep as 20 m, the values being greater than 100% of saturation. More significant than the actual depth is the fact that the maximum generally appears to be at, or more frequently just below, the halocline. It sometimes appears only at the inlet head, sometimes along the inlet length. The feature is observed most frequently in large-runoff inlets (Fig. 35(a) and (b)) but does occur in those with small runoff. It is not an invariable feature of either type or of a particular inlet. For instance it was observed in Bute in 1951 and 1954 but not in any of the other years from 1951 to 1960; it was observed in Toba in 1951, 1954, 1955 and 1958 but not in 1952, 1956 and 1957; in Jervis it was observed in 1952, 1954, 1958 and 1959 but not in 1956 and 1957. It is difficult to be precise about the location of the maximum because of the finite size of the water sampling bottles (0.3 to 0.45 m long) and their minimum practical spacing (1 to 1.5 m) but it appears that when the halocline is well defined, the oxygen maximum lies just below it and is sharply defined.

The layer of water whose oxygen content is above saturation is then only a few metres thick. At other times the oxygen maximum is much broader and the supersaturated layer may be 10 to 20 m thick (Fig. 36(a) and (b)). Both sharp and broad maxima have been observed (in different years) in the same inlet, e.g. Toba and Jervis.

Strøm's curves for many of the fjords in the southern coast of Norway (Strøm, 1936) show this feature of a maximum in oxygen content in the vicinity of the halocline, although the observations were at too few depths to determine any of the detail of the pattern of distribution.

The broad maxima are relatively common phenomena and the existence of a maximum below the surface (by day) is common in waters other than in these inlets. The explanation for the sharp maximum (e.g. Fig. 35(a) and (b)) is not known. Since the oxygen content is above saturation one must attribute it to phytoplankton, and the sharp differentiation between the surface brackish layer where the saturation is close to 100% and the deeper saline water where it is much higher suggests that the phytoplankton are limited to the saline water. The most remarkable feature is that this oxygen maximum is generally sharpest and has its highest value near the head of an inlet where the surface water is most turbid and therefore transmits least light. The maximum diminishes to seaward along the inlet where the water becomes less turbid and transmits more light.

The above-described maxima are clear anomalies from a condition of 100% or less saturation in the upper 30 m. Less well marked oxygen maxima are observed at 30 to 50 m in some inlets such as Gardner, Burke, Draney, Seymour,

Bute and Jervis. The oxygen content at these depths is always less than 100% and it is often difficult to say whether the maximum or the concomitant minimum is the more significant. Somewhat arbitrarily it has been decided to focus attention upon the minima rather than the maxima in the deeper waters and these are described in the next section.

5.3 OXYGEN MINIMA

In the cases discussed above where there is an oxygen maximum below the halocline, the surface value is smaller and constitutes one type of minimum. This is not regarded as particularly significant. Below the surface maximum, or the sub-halocline maximum, the oxygen content generally decreases to a value of 2.5 to 4 ml/l which is about 35 to 60% of the saturation value. In some cases the lowest value is at or near the inlet bottom, in others the deep water is nearly homogeneous in oxygen content (as well as in salinity and temperature) from a depth of 200 to 300 m to the bottom.

Most of the large-runoff inlets fall into one or other of the above two categories. Bute almost always has substantially homogeneous water from 300 to 650 m depth. Knight usually shows its minimum oxygen content near the bottom. In a minority of cases a slight mid-depth minimum appears. Such mid-depth minima, or sometimes just points of inflexion in the oxygen-depth curve, occur at the same depth as the bottom of the low temperature water forming the mid-depth temperature minimum layer (e.g. Fig. 37).

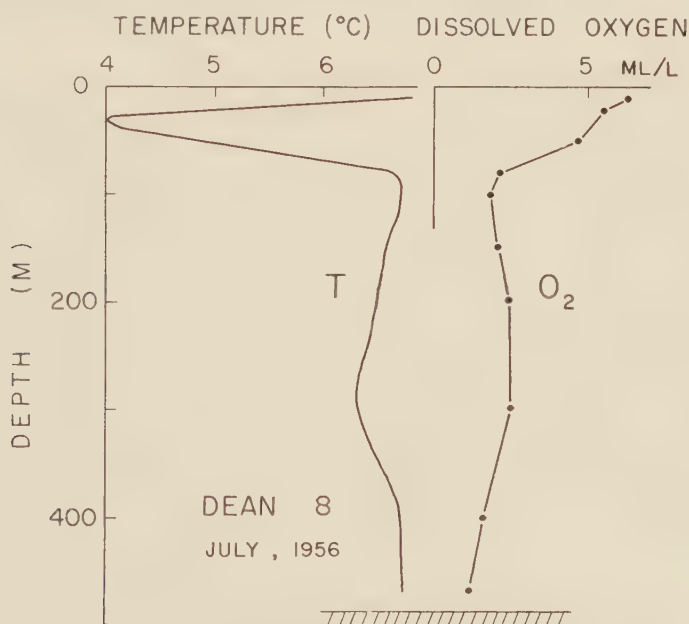


FIG. 37. Dissolved oxygen minimum below the temperature minimum at Sta. 8, Dean Channel.

Only a few inlets have water with an oxygen content of less than 1.5 ml/l. In Smith, in 1955 the oxygen content decreased to 1.2 ml/l at the bottom but only near the inlet head. Call has shown low oxygen values but the conditions in this inlet have varied from year to year. In Dean, in 1956 the oxygen content in the bottom water (161 m) at Sta. 10 near the inlet head was 0.5 ml/l. Between this station and the outer part of the inlet there is a sill with a maximum depth believed to be at 75 to 80 m and this presumably isolates the deeper water inside it. The measurements in 1951 did not extend as deep as those in 1956 but there was a marked decrease in oxygen content in the deeper water at Sta. 10 and 11.

Carter (1934) states that in Saanich Inlet, Princess Louisa Inlet, and the Narrows Inlet (of Sechelt) the "dissolved oxygen rapidly decreases to almost zero, [and] the density is greater than that of water at an equal depth in the Strait of Georgia". The observations in the present series do not entirely agree with this statement. The minimum oxygen content observed in Princess Louisa in 1952 was 1.7 ml/l at 140 m depth (the maximum depth in the inlet is 179 m). This was *greater* than that (1.5 ml/l) at the same depth in Jervis just outside the sill separating the two inlets. Furthermore, the oxygen content at lesser depths in Princess Louisa was considerably greater than that in Jervis, and not markedly different from values in the Strait of Georgia. In June 1960 the oxygen content to within 3 m from the bottom of the two basins of Princess Louisa was 3.3 ml/l compared to only 1.4 ml/l at the same depth in Jervis outside. Observations in the Narrows Inlet of Sechelt in 1957 did show a content of 0.15 ml/l at 1 m from the bottom, and the zero values in the deep water in Saanich have been mentioned previously.

In respect to the second part of Carter's statement above, the present observations disagree. As described previously it has been found that the density in basins such as Princess Louisa is *less* than that outside.

The most noticeable oxygen minima are those in the Belize-Seymour group and in Sechelt. In Belize there is an oxygen minimum layer which is most pronounced at the inlet head where the minimum value observed is 0.4 ml/l at 75 m. The distribution is shown in Fig 38(a) as a series of profiles and in Fig. 38(b) as a longitudinal section. The 8 miles at the head of Belize is an anomalous region. There appears to be very little runoff into it and the surface salinity is higher at the head than at Sta. 5 where Alison Sound joins Belize and presumably brings in the main fresh water flow. The Secchi-disc reading at the head of Belize is greater (up to 8 m) than further along the inlet (5 m) and the water is of an unusual yellowish-green colour. Thompson and Barkey (1938) observed a similar oxygen distribution at the head of Belize, with a minimum of 0.2 ml/l at 75 m depth.

In Seymour there is a less pronounced oxygen minimum of 2.5 ml/l between 150 and 180 m (Fig. 10). Again the observations of Thompson and Barkey showed a similar situation with a minimum of the same value at 150 to 200 m. Seymour differs from Belize in that there is an appreciable river runoff at its

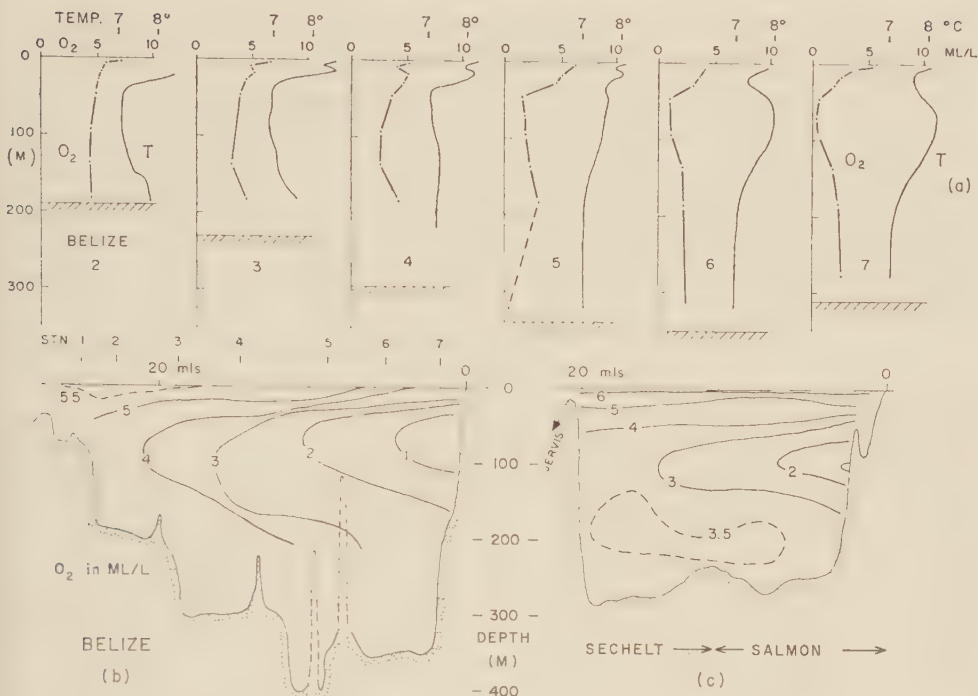


FIG. 38. (a). Vertical profiles of temperature and dissolved oxygen in Belize Inlet. (b and c). Longitudinal sections of dissolved oxygen in Belize and Sechelt Inlets showing mid-depth minimum.

head although the water is apparently not of glacial origin (Secchi-disc readings were as great as 5.8 m in 1951).

A very similar distribution to that in Belize was observed in Sechelt in 1957 with a minimum layer at about 100 m depth both in Sechelt Inlet proper (Fig. 38(c)) and in the connecting Salmon Inlet. The oxygen minimum was more pronounced (1.3 ml/l) in Salmon than in Sechelt (1.4 ml/l).

Thompson and Barkey (1938) suggested that the mid-depth minimum was due to a flow of water from a shallower section of an inlet, or from a side arm, where it had been in contact with a reducing bottom. Although this seems to be a logical explanation, the details of a circulation to maintain this distribution are not clear. The character of the low oxygen content tongue suggests flow away from the head of the inlet toward the mouth and this requires a supply of mid-depth water to the head. The only likely source of this mid-depth water is by sinking of shallower water and it is considered that the head of the inlet is generally the least likely place for this to occur because of the relatively low density of the water above the oxygen minimum compared with elsewhere in the inlet. The real questions are why the oxygen minimum should be at mid-depth and not at the bottom in these inlets, and why this distribution occurs in only a

few inlets. The area of bottom with which the water at the oxygen minimum level is in contact is only a small fraction of the whole bottom area. One suggestion offered here is that reduction takes place over the whole bottom volume for some years until eventually an intrusion of saline water of sufficient density to displace the bottom water upward occurs. At the same time the greater tidal currents near the mouth might cause greater mixing and more rapid dissipation of the low-oxygen water than at the head. In this case the tongue at the head would represent a vestigial remnant of a layer which earlier spread over most of the inlet bottom. However, the fact that almost identical distributions were found in 1951 as in 1937 in Belize and Seymour suggests that the observed distribution is a steady-state one and that some continuing process for its maintenance must be assumed to exist.

An alternative suggestion, favoured by the author, is that the mid-depth minimum is a consequence of several simultaneous and continuous processes. Sinking organic material along the full length of the inlet may use up oxygen in the subsurface water. At the same time small but frequent inflows of oxygenated saline water from outside may take place over the entrance sill and spread over the inlet bottom, so that the oxygen-deficient water is held at mid depth. In addition, the maximum tidal currents are near the mouth of the inlet and therefore vertical mixing is probably greatest there, tending to eliminate the oxygen minimum and leaving it more conspicuous at the inlet head. The inlets in which the mid-depth minimum occurs are ones with small fresh water runoff and consequently the induced estuarine circulation is not sufficient to replace the oxygen deficient layer entirely, as it does in the large-runoff inlets. Another contributing factor may be that the relatively low stability in the upper layers in these inlets may aid vertical mixing to reduce the density of the deep waters. This would mean that water from outside at sill depth could be denser than even the deepest water in the inlet basin and hence it could sink along the bottom after entry.

It is suggested that a comparison of the bottom sediments near the inlet head at the oxygen minimum level in Belize and Sechart with other inlets not showing the minimum might be profitable, and a study of the mid-depth oxygen minimum might yield useful information on the circulation in the inlets.

One other locality in which very low oxygen values were found was in Minette Bay at the head of Douglas. It is a basin some 3 miles long by $\frac{3}{4}$ mile wide, supplied by small streams. The maximum depth measured was 38 m and Minette is connected to Douglas by a shallow channel only a metre or so deep at low water. The salinity and temperature of the water in Minette in 1951 corresponded to that at the head of Douglas but the oxygen content was less. It decreased from 6.9 ml/l at 3 m to 0.55 ml/l at 25 m, compared to 6.9 ml/l and 4.9 ml/l in Douglas at the same depths.

6. OPTICAL TURBIDITY

6.1 OPTICAL TURBIDITY OF THE SURFACE WATERS

A conspicuous visual feature of the inlet waters is the colour and the turbidity or otherwise of the upper layer. In the inlets which receive runoff from glacial rivers, the surface water at the head during the summer is milky white in appearance and of high turbidity. It changes through a milky green along the inlet to green with a lower turbidity near the mouth. In contrast, in the inlets which do not receive much runoff the water is green and of more or less uniform and lower turbidity along the whole length of the inlet. (In the inner reach of Belize in 1951 the water was of an unusual yellowish colour.)

In Table XI are listed values of the Secchi-disc depths in the majority of the inlets during the runoff period, May to September. For some inlets visited a number of times (e.g. Bute, Knight) the range of values observed is quoted. The first group of inlets includes those for which the large rivers are definitely glacial in origin, those of the second group receive runoff from large rivers to which the glacial contribution is believed to be small or negligible, while the third group includes those having relatively little runoff at all.

In Fig. 39 are shown values of Secchi-disc depths for some typical examples of the three groups in Table XI. For Gardner and Knight the small values toward the head are also shown on an enlarged scale. For Jervis values for 2 years show the differences observed in inlets with small rivers, while Kynoch and Work are examples of very-low-runoff inlets.

Vancouver (1798, Vol. I, pp. 304, 305, 308, etc.) was probably the first to draw attention to the white appearance of the water at the heads of some of the inlets, e.g. Howe, Bute, Knight, Kingcome, but not Jervis. On first observing it in Howe he "attributed [it] to the melting of the snow, and its water passing rapidly over a chalky surface, which appeared probable by the white aspect of some of the chasms that seemed formerly to have been the course of water-falls, but were now become dry." Later he noted that in Jervis "The cataracts here rushed from the rugged snowy mountains in greater number, and with more impetuosity than in Howe's sound; yet the colour of the water was not changed, though in some of the gullies there was the same chalky aspect. Hence it is probable, that the white appearance of the water in Howe's sound, may arise from a cause more remote, and which we had no opportunity of discovering." Vancouver's observations and deduction were acute and it is probably only because his instructions forbade him from making excursions up the rivers that he was prevented from determining the "cause more remote". This is the grinding of rock against rock in the motion of the glaciers on the mountains which produces a finely divided "rock flour" which is brought down by the rivers. Much of this remains in suspension for a considerable time and is carried along the inlet by the outflowing surface layer. During the winter months the water in the greater part of the length of Bute is relatively clear and greenish in colour. Then in the spring when the runoff starts (usually in May) a sharp front of silty water moves

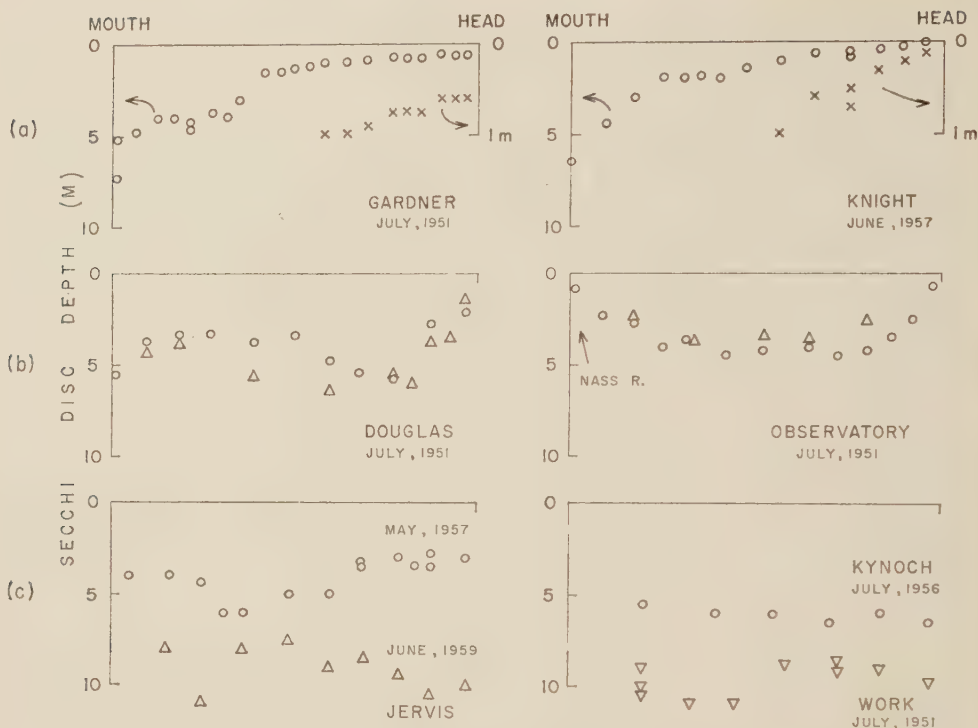


FIG. 39. Longitudinal profiles of Secchi-disc depths in large and small runoff inlets.

down inlet in a few days and for the rest of the spring, summer and fall the water has its characteristic silty appearance. Occasional observations while skin diving in these inlets have shown that near the inlet head the lower boundary of the silty surface water is quite sharp and appears to be close to the halocline. A very marked increase in the clarity of the water is evident when one swims down through the halocline-thermocline into the more saline water below. When the silty layer is only 2 to 3 m thick, the propeller of a ship will often bring the clear water to the surface and the track of a vessel moving near an inlet head may remain visible for some time. In such a region, when a Secchi disc or a bucket is lowered through the silty layer and then pulled smartly back to the surface it will bring with it a "bubble" of the clearer saline water.

The illumination in the clear water below the silty layer is much greater than would be calculated from the loss of light in the upper layer on the basis of an absorption coefficient k obtained from the Secchi-disc reading D using the formula $k = 1.7/D$ determined by Poole and Atkins (1929). For example, for a typical value of $D = 0.3$ m, the formula yields $k = 5.7$, and for a silty zone thickness of 4 m the illumination below this zone would be reduced to about 10^{-10} of that at the surface. That is, for full sunlight at the surface (about 10^4 foot-candles) the illumination below the silty water would then apparently be reduced to about 10^{-6} f-c, or about one-hundredth of the illumination on a clear

TABLE XI. Secchi-disc depths in British Columbia mainland inlets (May-September).

Inlets	Mouth	Middle	Head
Inlets with large river of glacial origin:			
Portland Canal	3.5	2.5	0.3
Portland Inlet	2.5	...	1.0*
Gardner	6	1.5	0.6
Dean	3-6	1.5-3.5	1.0
Burke	2.5-6	5-5.5	0.4
Rivers	4.5	3.5	1
Kingcome	1.5-3	...	0.5
Knight	4-8	1.5-4	0.1-0.5
Bute	3-8	1.5-3	0.1-0.3
Toba	4-6	1-3	0.3-1
Howe	3	1.5	0.5
Inlets with large rivers having small glacial contribution:			
Observatory-Alice	1*	4	3
Douglas	4	5.5	2
Inlets with small rivers or streams only:			
Work	10	8.5	9.5
Surf	6	6	6
Laredo	7.5	6.5	7.5
Sheep-Mussel	3	6	5.5
Matheison-Kynoch	5.5	6.5	6.5
Spiller	5	7	5
Roscoe	7	7.5	6
Cascade	6	8	7
Draney	5	5	...
Smith	3.5	4.5	4.5
Belize	4.5	5.5	7
Seymour	5	8	5
Call	3.5-9	...	4.5-8
Loughborough	3-6	4-8	3-10
Pendrell	6-9	7-10	7-9
Jervis	4-6	6-10	3-10
Sechelt	6	5.5	3.5
Indian	4	7	6.5

*The Nass River enters at the junction of Portland Inlet (head) and Observatory Inlet (mouth).

starlit night. Direct observation indicates that the illumination is much greater than this. It might be inferred that the formula of Poole and Atkins, which was determined for Secchi-disc readings of 10 to 50 m, gives too large a value for the absorption coefficient at the very small Secchi-disc readings observed in the inlets. However, measurements of the turbidity described in the next section yield even greater values than 5.7 for the scattering coefficient τ which is related to k . The probable explanation for this apparent paradox is that the quantities k in the Poole and Atkins formula or τ in the next section properly describe the rate of loss of light from a narrow parallel beam of light by scattering out of the beam

as well as by true absorption which implies conversion to some other form of energy. This is not the case at the head of an inlet where the surface layer is very extensive in relation to its thickness and light is passing through all parts of it. Then at any small area at the lower surface of the silty layer the part of the light which has been lost by scattering from the direct beam to that area is to some extent replaced by light scattered from neighbouring beams. The illumination is therefore not reduced as much as it would be if true absorption occurred to the extent of the k or τ values calculated.

The decrease of Secchi-disc readings toward the mouth of some inlets can often be attributed to the effect of phytoplankton blooms which are common in the spring and summer.

The relatively low turbidity in Burke seaward of Sta. 8 supports the suggestion made on the basis of surface salinity that a large proportion of the runoff into the North and South Bentinck Arms (head of Burke) moves out through the connecting Labouchere Channel into Dean, rather than along the seaward reaches of Burke.

6.2 OPTICAL TURBIDITY OF THE SUBSURFACE WATERS

Measurements have been made of the turbidity of both surface and deeper water in some of the southern inlets and the results have been described previously (Pickard and Giovando, 1960). As some of the observations and the conclusions from them are relevant to the present description of inlet water properties they are summarized here.

The measurements were made on board ship by means of a commercial light-scattering microphotometer on samples obtained with reversing water bottles internally coated with ceresin wax to reduce contamination of the water sample by particulate material from the metal bottles. A light-scattering method was used, rather than a transmission method, in order to see how much information could be obtained on the nature of the particulate material in the water, as well as on the turbidity or light attenuation itself. One object in making the measurements was to investigate the possibility of using the turbidity as a tracer of deep water movements.

Polar diagrams of the scattered light show predominantly forward scattering with a broad minimum from 100 to 120° from the forward direction of the light beam through the sample. There is little difference in shape of the polar diagram with turbidity or wavelength of light, confirming that the particle size is generally large compared to the wavelength of light. Polarization measurements indicate that the material is optically anisotropic. These results suggest that the material is largely that brought down by the rivers from glacial abrasion of the granitic rocks in the region, the "rock flour" referred to above.

A number of typical samples have been filtered through 0.5- μ "Millipore" filters. The water passing through these filters has a very low turbidity, not much greater than that of distilled water, indicating that there are very few particles smaller than 0.5 μ diameter in the inlet waters. The particles retained by the filters appear to be chiefly minerogenic in character with a size range from 0.5 to 50 μ .

In Table XII are given some typical values of turbidity of the water and corresponding particle size. The turbidity τ is defined by the usual equation:

$$I = I_0 \times e^{-\tau L}$$

where I_0 and I are respectively the incident and emergent intensities of a beam of parallel light passing through a layer of thickness L metres of water of turbidity τ expressed in reciprocal metres (m^{-1}). Measurements were made with green light (5460 Å) for all samples and with other wavelengths for some.

TABLE XII. Mean values of optical turbidity in waters of Jervis and Bute Inlets for winter and summer, and of size of particulate material in Bute.

Depth (m)	Winter		Summer	
	Jervis Inlet optical turbidity (m ⁻¹)			
	Outer basin	Inner basin	Outer basin	Inner basin
0-50	0.14	0.9	2	11
50-250	0.1	0.2	0.6-0.9	2
250-600	0.1	—	1-1.3	—
Bottom	0.15	0.45	1.3	3
	Bute Inlet optical turbidity (m ⁻¹)			
	Mouth	Head	Mouth	Head
0-50	0.2	0.7	7	18
100-550	0.10	0.12	0.7	0.7-1
550-650	0.16	0.4	0.9	1.5
	Bute Inlet particle size (microns)			
Mean:	7	10.5	8	17
Range:	0.5-15		0.8-49	

Volume concentrations of particulate material range up to 105 ppm and weight concentrations to 285 ppm. The material is 90% minerogenic in winter and 99% so in summer.

The major features of the turbidity distributions are (a) the difference between large- and small-runoff inlets, (b) differences between values at different depths in a vertical column at any point, (c) seasonal variations in both types of inlet.

Bute and Knight both show larger values of turbidity than Loughborough and Jervis at similar depths. This is in accord with the observation that the particulate material is chiefly glacial rock flour. The largest turbidity values are found at the heads of the inlets in the low-salinity surface layer. The values in the main body of the water in an inlet between the surface layer and a layer near the bottom are generally fairly uniform. Values in a layer 50 to 100 m thick in contact with the bottom are often higher than in the main body above. The seasonal variation in turbidity values is evident in both large- and small-runoff inlets.

From the above findings it is concluded that the rivers flowing into the inlets are the chief source of particulate material in the inlet waters. The silt

introduced by the rivers is carried along in the surface layer which acts as an extended source of particles which shower down into the main body of water. For this reason the turbidity has severe limitations as a tracer of deep water influx from outside.

The increase of turbidity near the bottom is interesting. In describing a similar distribution in the shallow Gullmar Fjord, Jerlov (1953) attributes it to the stirring action of tidal currents. However, such data as are available for the deeper British Columbia inlets (Pickard and Rodgers, 1959) suggest that the bottom currents in these flow at only a few centimetres per second and are unlikely to be sufficient to maintain material in suspension in a layer of 50 to 100 m depth. An alternative hypothesis favoured is that the increase in turbidity near the bottom is a consequence of mud slumps on the slopes at the head of an inlet starting turbidity currents which flow along the inlet bottom. There are several pieces of evidence to support this hypothesis. For instance, in Bute the high-turbidity bottom layer stops abruptly at the sill. It is less common in the outside passages where tidal currents may be expected to be greater. In Jervis, the increase near the bottom occurs only inside the inner sill where tidal currents should be least. Another point is that in many inlets there is an area of flat bottom in the deepest part of the basin inside the sill (ref. Sub-sect. 2.1, page 914). These flat areas are probably the result of settling out of material from turbidity currents trapped by the sill. There is no other source of the material in these regions than the mud banks deposited by the rivers at the inlet head. A third point is that the water in Bute and other inlets, below sill depth, is generally nearly homogeneous despite the evidence of inflow of deep water from outside from time to time. This homogeneity may be attributed to the stirring action of the turbidity currents. The fact that the increase of turbidity near the bottom was evident in each survey, combined with calculations of settling rate, suggests that these turbidity currents occur quite frequently.

From the difference between winter and summer concentrations of particulate material, it is possible to calculate an average rate of deposition of sediment of 35 cm per 1000 years. Near river mouths the value may be as high as 600 cm per 1000 years.

7. WIND AND WAVES

7.1 WIND AND SURFACE WAVES

The wind can be expected to affect oceanographic conditions in the inlets in several ways. The frictional stress on the surface influences the motion of the surface layer and so may increase or decrease the mean surface-layer flow along an inlet. In addition, the waves generated by the wind will cause mixing in the surface layer tending to make it homogeneous. During the cruises therefore, observations of wind velocity were made at each station by means of an anemometer at 4 to 10 m above sea level, and the significant wave height was estimated visually at the same time. In Table XIII are presented these correlated wind-wave data for the cruises from 1951 and 1959 all lumped together. The totals

TABLE XIII. Frequency of occurrence of wind speeds and wave heights in British Columbia inlets for summer months from 1951 to 1959 inclusive (percentage of 1653 observations).

Wave height		Wind speed					Wave-height frequency totals
Beaufort scale	Feet	Beaufort force: 0 and 1 Knots:	2 and 3 0-3	4 and 5 4-12	6 13-24	7 25+	
		%	%	%	%	%	%
0	Calm	27	4	0	0		31
1	0 to 1	14	28	5	0		47
2	1 to 3	1	5	14	$\frac{1}{2}$		20 $\frac{1}{2}$
3	3 to 5	0	0	1	$\frac{1}{2}$		1 $\frac{1}{2}$
Wind speed frequency totals:			42	37	20	1	100

have been normalized to show the percentage frequency of occurrence of the stated ranges of wind speed and of wave height and of the combinations thereof. The data for individual cruises vary considerably from these means but there does not seem to be any significant pattern and therefore the details are not presented. 95% of the observations were made during daytime between about 0600 and 2000 hours.

It is seen that for about 80% of the time during the summer the wind speed is not over 12 knots nor the wave height greater than 3 feet. It may be added that on no occasion during summer cruises have oceanographic observations been prevented by wind or waves, although there have been occasions when the drift of the ship due to the wind has caused some anxiety for the safety of equipment over the side when operating in these narrow inlets where the depth often changes considerably in a short distance. The waves referred to in Table XIII are all short-period (2- to 4-second) wind waves or "sea" generated locally in the inlet and progressing along the inlet, i.e. with their crests approximately at right angles to the longitudinal axis of the inlet. At no time is there any indication of "swell" or long-period waves penetrating from the ocean. For this reason, shipboard operations are not hindered by rolling of the ship, except on rare occasions at anchor station when, due to the opposing action of wind and current, the ship lies across-inlet and therefore parallel to the waves. The stability of even a small vessel permits operations and the use of instruments which would be quite impossible in less protected waters. This is an important factor to bear in mind when considering the practicability of equipment for oceanographic work in these regions.

The wind direction in the inlets is almost invariably along the length of the inlet, following the bends, and most often directed *up*-inlet during the summer. The along-inlet direction of the wind is a consequence of the channelling action of the steep sides of most of the inlets. In addition the wind speed is significantly affected by the inlet width, and an increase of wind speed is often experienced in the narrower, steeper-sided reaches. This is probably of some consequence since in a narrow part of the inlet the speed of the surface flow will also increase and there is likely to be increased turbulence. This, with the increased wave

action due to the stronger wind, promotes mixing in the upper layer and therefore such narrow portions of an inlet may be regions where much of the mixing takes place. The wind speed is generally greatest near the mouths of the inlets and least near the head. The up-inlet wind is usually diurnal in character, springing up during the morning and dying away in the late evening. Ship operations are therefore often facilitated by scheduling work in the seaward reaches of an inlet for the early morning and working up to the head in the afternoon.

7.2 INTERNAL WAVES

During the first cruise in 1951 it was observed that the depth of isotherms at a fixed station showed distinct variations with time. In the upper layers (5 to 20 m) these oscillations had periods of 1 to 3 minutes, while at mid-depth (50 to 100 m) the period appeared to be several hours. These observations were verified and extended in subsequent cruises and there is no doubt that in the upper layer the vertical oscillations are the result of progressive internal waves occurring in the pycnocline associated with the halocline (Pickard, 1954). The precise character of the mid-depth oscillations is not yet determined but for convenience both these and the shallow ones are referred to as internal waves. The observations in subsequent years have confirmed that both the shallow and the deeper internal waves are common features in some inlets.

7.21 SHALLOW INTERNAL WAVES

These were observed on a number of occasions in Knight particularly, and measurements of their amplitude and apparent period were made with an electrical resistance thermometer using a thermistor bead on the end of a cable marked in metres. With this device the depth of an isotherm in the thermocline was followed and recorded at short intervals to reveal the characteristics of the shallow internal waves. This was done on a number of occasions when the sea state was slight and the ship so steady that variations in the length of cable out could be taken as variations in depth of the selected isotherms. Sample records of these internal waves are shown in Fig. 40 together with a record showing typical "quiet" conditions. On the records obtained, the intervals between successive crests range from 1 to 5 minutes. Although it is tempting to identify these intervals with the periods of the waves, it must be pointed out that when the waves occur between the surface low-salinity layer and the deeper more saline water both of these layers are generally in motion, often in opposite directions as a result of estuarine and tidal currents (Pickard and Rodgers, 1959). Since the observations were usually made from an anchored ship, the observed time intervals between wave crests might differ from the true period of vertical oscillation of a water mass. When current measurements were available at or close to the time of the internal wave oscillations it was estimated that the observed time intervals probably did not differ from the true period by more than a factor of $\frac{1}{2}$ to 2. The wavelengths of the waves were estimated from associated surface manifestations ("ruffled bands" described below), either in relation to ship's

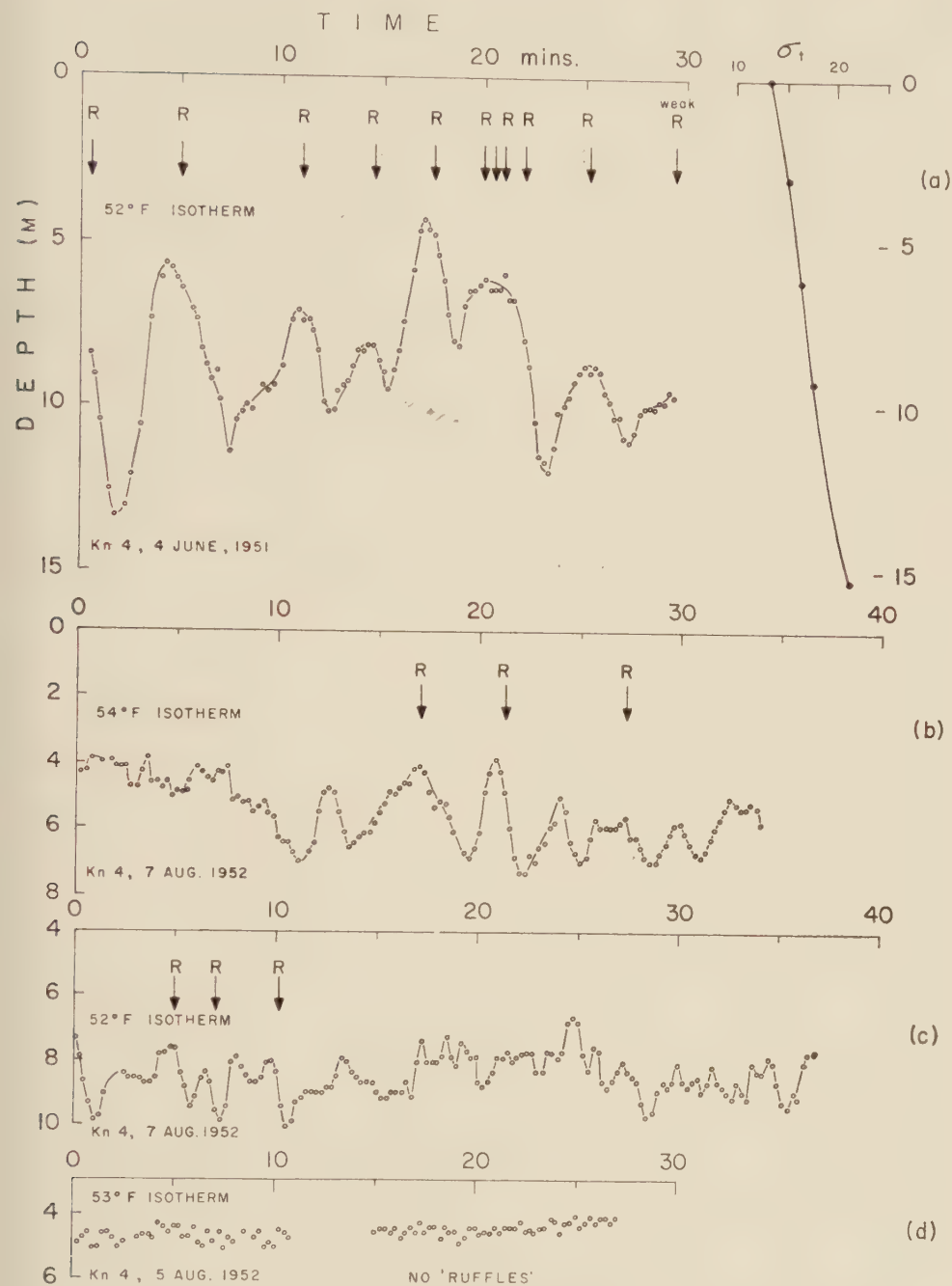


FIG. 40. Time-depth plots for selected isotherms in Knight Inlet to show the presence (a), (b), (c) or absence (d) of shallow internal waves.

length or by time and ship's speed when sailing. They were between 50 and 200 m. The speed of travel in still water would then be about 1 m/sec.

The appearance of the sea surface accompanying these shallow internal waves is quite striking and merits description. On a calm day, when the sea surface is otherwise mirror smooth, the internal waves are accompanied by a series of narrow (10 to 30 m wide) "ruffled" bands on the water with wider smooth patches in between. These ruffled bands stretch across the inlet and usually progress with a speed of up to 1 m/sec relative to the shore. They are generally located just behind the advancing internal wave crest as observed with the thermometer. The word "ruffled" is used to describe the bands since the surface asperities do not consist of series of ripples such as those generated by the wind but of randomly distributed peaked protuberances of some 5 to 10 cm height. The passage of the ruffled band is accompanied by a characteristic hissing noise similar to that caused by rain falling on water. It appears to be due to water from the peaks of the ruffles breaking off and falling back into the water. When these ruffles have been seen in calm water it becomes quite easy to pick them out even when superimposed on wind waves up to 3 feet height. The explanation suggested for these ruffles is that they indicate the location of the region of convergence behind the crest of the moving wave (e.g. Sverdrup *et al.*, 1942, p. 588). In many cases in the inlets, the amplitude of the waves in the halocline is comparable to the mean depth of the halocline and consequently the convergence is very strong. The motion of the water in the upper layer is often made evident by the motion of the ship relative to the hydrographic wire if the latter extends an appreciable distance into the relatively stationary deeper water. If the ship happens to be lying parallel to the wave crests, the wire will alternately trend under the ship and then away from the ship as the latter is moved back and forth by the surface flows associated with the internal waves. The presence of these internal waves may be indicated by an apparently anomalously large hysteresis at the thermocline in bathythermograms taken at the time. This evidence often reveals the presence of internal waves even if their amplitude is not large enough to make the ruffled band effect conspicuous. Some idea of the amplitude of the internal waves may be obtained by lowering a bathythermograph through a ruffled band and then raising it through the succeeding smooth patch, or vice versa. There is little point in attempting to make a conventional bottle cast in the upper 50 m or so when such internal waves are evident, and as the hydrographic wire is likely to be carried under the ship it is prudent to suspend operations with overside equipment in the presence of such waves.

It should be made clear that the surface phenomenon just described and interpreted differs in detail from that described by Ewing (1950), although both are associated with the convergence in the surface layer accompanying internal waves. The essential difference is that the phenomenon described here consists of narrow bands of ruffles on otherwise smooth water, whereas Ewing describes narrow slicks or smooth bands on otherwise wind-rippled water. Ewing ascribes the slicks to the ripple-smoothing action associated with surface contaminants being concentrated by the water convergence, whereas the effect observed in the

British Columbia inlets is ascribed here to a purely mechanical process in the intensely convergent water flow. The slick patterns described by Ewing have been observed frequently by the author in local coastal waters, for instance in English Bay near Vancouver, but rarely in the inlets.

The shallow internal waves have been observed most frequently in the vicinity of the sill (between Sta. 3 and 4) in Knight. Current measurements in this region (Pickard and Rodgers, 1959) have shown that at times a strong shear develops between the low-salinity surface layer flowing seaward and the deeper more saline water, particularly during the first part of the flood tide. The waves are sometimes observed at other times than this however. They are not often observed more than about 10 miles from the sill in Knight, presumably having dissipated their energy within this distance. Similar waves are sometimes observed in Bute near Sta. 2 and are probably associated with the strong currents flowing in through Arran Rapids where water from the northern passages enters the inlet. Surface ruffles have also been observed by the author in Burke and in Observatory. Comments in the British Columbia Coast Pilot (Canadian Hydrographic Service, 1953, p. 2) suggest that they may be common in Burke (although the phenomena described in the Pilot are not there interpreted in terms of internal waves). Annotations on Admiralty Chart 2458 together with the strong ship movement experienced during a University of British Columbia oceanographic cruise in Observatory suggest that internal waves occur frequently in the latter.

On calm days when there is a distinct surface layer of 2 to 3 m depth it is quite common when the ship is brought to a stop at a station to see a series of several ruffles move on ahead and to the beam of the ship as it comes to a halt. These are assumed to be associated with bow waves generated by the ship at the internal boundary as it slows down through the speed of propagation of internal waves at this boundary.

When flying over the southern Strait of Georgia in the spring and summer, when the water is stratified due to the runoff of the Fraser River, one frequently sees extensive systems of ruffles apparently originating at the passages between islands in the southern part of the strait. Shand (1953) has described this phenomenon and interpreted it as evidence of internal waves. Although simultaneous measurements in the water were not available to him there is no doubt that his explanation is correct as the writer has observed the phenomenon at close hand while making current observations in the strait. In this region the surface layer is usually turbid while the deeper water is much clearer. Under these conditions, internal waves are often visually evident as a series of turbid bands (over the troughs of the internal waves) separated by darker bands (of clearer water over the crests of the waves). A similar distribution of turbid (low-density) water overlying clearer (more dense) water is found regularly toward the heads of the inlets but internal wave evidence has not been observed. This is possibly because no generating mechanism in the form of a marked shear flow occurs in these localities.

7.22 MID-DEPTH INTERNAL WAVES

The mid-depth internal waves have been observed on many occasions in Bute and Knight and appear to be a regular feature. A good example of the observed phenomenon is shown in Fig. 41. The data for the Figure were obtained in Bute by making bathythermograph casts at 30-minute intervals for about 3 days

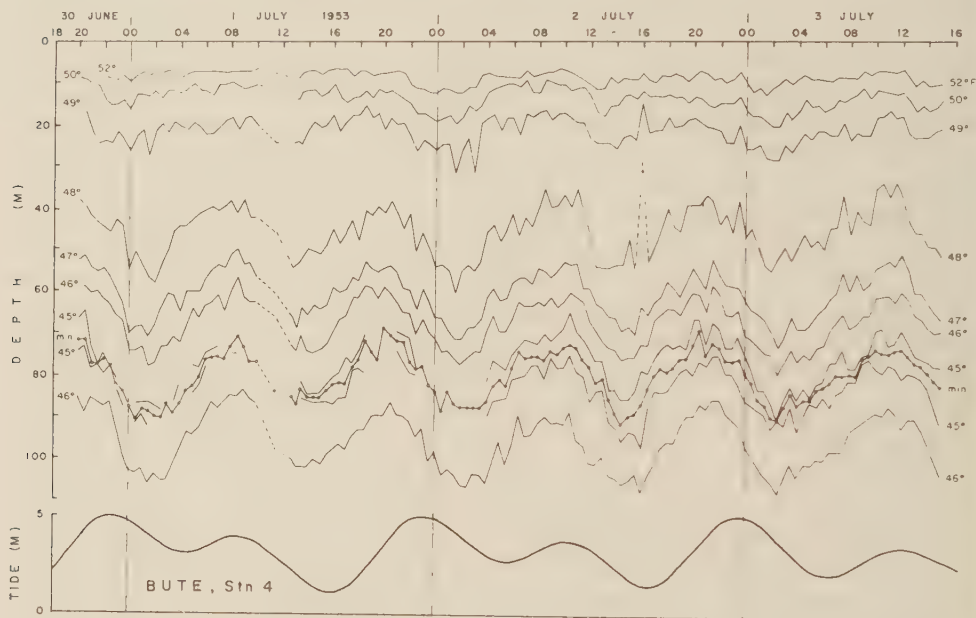


FIG. 41. Time-depth plots for isotherms in Bute Inlet to show the presence of mid-depth internal waves.

when there was a well developed temperature minimum (see Fig. 19). The marked gradient of temperature with depth above and below the minimum made it practicable to read off the depth of selected isotherms from the bathythermograms (T - z profiles) with fair accuracy and from these readings time series plots such as that in Fig. 41 were made. The isotherms at depths greater than about 40 m show both a gross variation in depth with time and a fine structure. The gross oscillation is seen to have a period similar to that of the surface tide and to be about 40° advanced in phase. The fine structure may either be real or be indicative of the possible inaccuracy of the method as used to determine the depth of a particular isotherm, or be a combination of both. Real short-period fluctuations in depth of a given isotherm about its mean value could be due to and indicative of turbulent motion of the water. Apparent short-period fluctuations could be attributable to instrumental inconsistency, improper technique in inserting the slide in the bathythermograph, or to errors in reading the bathythermograph. The only likely error in technique is to fail to push the slide fully home when inserting it in the bathythermograph. The

result is then a decrease in apparent depth of isotherms above the temperature minimum and a simultaneous increase in apparent depth below the temperature minimum when the slide is read in the viewer. An isolated example of this is apparent in Fig. 41 at 1600 hours on July 2. To investigate the personal errors, several series of bathythermograms were read and time series plots prepared independently by different individuals. Differences certainly were found between such plots, particularly at depths where the temperature gradient was small, but at the same time much of the fine structure was found to be common to the independently prepared plots. This suggests that human error in reading is not entirely responsible for this feature, but it does not determine the relative contributions of instrument inconsistency and of real fluctuations in depth. However, most of the series of observations were made with selected bathythermographs having small hysteresis and histories of close correspondence with temperatures determined with reversing thermometers. Sometimes a recognizable detail in the bathythermogram could be tracked for several hours, and its vertical motion generally followed that of the isotherms near to it. It is therefore considered probable that the fine structure on the plots has some reality.

It has not proved possible to follow oscillations at depths much greater than 100 to 120 m by this simple technique because the temperature gradient becomes too small for the depths of isotherms to be read with any confidence. At depths of less than about 20 m the vertical oscillations become too small and too rapid to be followed conveniently by this bathythermograph method because the stability of the water becomes very great. A more sensitive electrical resistance type of thermometer, or an isotherm-follower of the type described by LaFond (1961) would be useful to extend the observations of these mid-depth internal waves.

The observed amplitude of the vertical oscillations varies from series to series. In Fig. 41 the total amplitude of vertical oscillation in the vicinity of the temperature minimum is about 20 m with the amplitude decreasing at lesser depths. In other series the amplitudes have been from 5 to 75 m.

The interpretation of these time series observations is not certain. Possible explanations are that (a) they are evidence of progressive internal waves, (b) they are evidence of standing internal waves, (c) they are simply an incidental consequence of the back-and-forth tidal movement of water having isotherms inclined to the horizontal along the length of the inlet.

The last alternative is rejected for two reasons. The required longitudinal inclination of the isotherms to the horizontal is not generally observed either in regular surveys along the inlets or in special quasi-synoptic series made by taking a series of bathythermograph casts rapidly at half-mile intervals through the anchor station positions. The data at present available do not permit one to distinguish between alternatives (a) and (b). All but one set of observations have been made by a single ship at any one time. This set consisted of simultaneous observations in Bute at two points approximately one quarter and one half the length of the inlet from the head and it revealed internal waves out of phase by 180° within the accuracy of observation. This could be explained either

in terms of progressive waves, or of standing waves with a node between the two observation stations. A critical experiment would be to make a series of simultaneous observations at two points at different separations to see if the phase difference varied continuously along the inlet at any instant (progressive waves) or had eigenvalues of 0° or 180° only (stationary waves).

The density distribution in the inlets is such that, except for the wind mixed surface layer of a few metres depth, the water is always gravitationally stable. The free period of vertical oscillation of a small mass of water calculated from the observed density gradient ranges from about half a minute in the halocline at 5 to 10 m depth to one hour at 300 m depth (see Fig. 28). These values are much smaller than the gross period of oscillation observed in the time series, but of the same order as that of the fine-structure components (as far as can be judged from observations at 30-minute intervals).

If the observed continuous density distribution is approximated by a two-layer system with an upper layer of thickness 100 m and average density difference of 1 mg/cc less than that of the deeper layer, and if Bute is regarded as a narrow bay closed at one end, the fundamental free period of an internal seiche at the boundary between the two layers would be about 8 hours and for a 50-m depth of upper layer it would be about 10.5 hours. Corresponding values for Knight would be about 11 and 14 hours. Such a two-layer approximation is crude, though the density difference is realistic, but it suggests that it is not unlikely that mid-depth internal waves could occur, being driven by the tidal in-and-out flow in some manner.

These internal oscillations present interesting problems in themselves as to character and origin, but will need further properly designed observations for their elucidation. However, their frequent, if not invariable, occurrence must be borne in mind when longitudinal profiles of water properties are being considered. Without carrying out anchor stations during each survey of an inlet it would not be possible to eliminate the effect of the waves on apparent distributions of properties. In this connection it may be noted that when using conventional oceanographic techniques for water sampling from a 10-knot ship the time taken to complete eight oceanographic stations along the 40-mile length of Bute Inlet is 8 to 9 hours, a time of the same order as the period of the internal waves.

8. BUTE INLET WAX

About six times between 1922 and 1956 there have been reports of the appearance in Bute Inlet and occasionally at the mouth of the neighbouring Toba Inlet of a peculiar whitish waxy substance. The material appears only during some unusually cold winters and is then found on the shore and floating on the water in amounts variously reported as "bucketsful" to "scow loads". Examination of the material at the Fisheries Research Board of Canada Technological Station, Vancouver, (Anon., 1951) has shown the substance "to be essentially a wax, i.e., fatty alcohols combined with fatty acids. The wax contains almost no

glycerides, which are the major components of fish and marine mammal oils. It contains little, if any, hydrocarbons, which are the substances composing petroleum". The wax solidifies at about 11°C, its specific gravity is 0.87, and carbon-14 determinations give its age as 0 to 300 years (Swain, quoted by Williams, 1957). Above 11°C it is a brown liquid.

Williams has assembled the available information on the wax. He draws attention to the fact that one half of the total stands of lodgepole pine in British Columbia occur in the watershed of Bute Inlet and that the pollen is often observed in considerable quantities on the water in Bute but not elsewhere. He suggests that it is possible that the wax may be a decomposition product of this pollen.

The wax has not been reported from any other region in British Columbia and neither Williams nor the author has been able to find in the literature any description of such a material being found elsewhere. Any hypothesis to explain its occurrence must take into account, since the wax is lighter than water, the fact that the surface layers of water in the inlet have a net motion out of the inlet both in winter and in summer.

9. SUMMARY AND DISCUSSION

The oceanographic studies of the inlets of the mainland coast of British Columbia have shown that as a consequence of the precipitation and the discharge into them of fresh water from rivers they are all essentially positive estuaries, the salinity of the water ranging from zero to that of the coastal waters outside. The inlet waters are markedly stratified and the density is determined chiefly by the salinity. The circulation in the inlets appears to be dominated by the influence of the river runoff, and in fact the differences between property distributions from inlet to inlet can be explained as a direct consequence of the fresh-water-induced estuarine circulation.

The inlets are often compared to the Norwegian fjords. Morphologically the comparison is appropriate but in one respect at least they differ—very few, if any, of the British Columbia mainland coast inlets are sufficiently stagnant to exhibit anaerobic conditions. Before pursuing this point one comment should be made. A frequently quoted reference for descriptions of Norwegian fjords is the paper by Strøm (1936), but it sometimes appears to be forgotten that this valuable paper was not intended to be a general description of Norwegian fjords. Its title is "Land-Locked Waters: hydrography and bottom deposits in badly-ventilated Norwegian fjords with remarks upon sedimentation under anaerobic conditions". Strøm restricts himself to the fjords in the southern quarter only of Norway's coastline, and further restricts himself to those which might be expected from their depths to be stagnant. Not all of those studied proved to be stagnant and Strøm presumably deliberately omitted the greater fjords, such as Sogne Fjord and Hardanger Fjord, in the region studied. The coast north of that studied by Strøm contains many fjords, and his paper is not and was not intended to be broadly descriptive of Norwegian fjords as a whole. To get a more complete

picture of the Norwegian fjords it is necessary to refer also to other descriptions such as those of Mohn (1887), Nordgaard (1899, 1903), Gaarder (1915) and others. These indicate that many of the fjords are not stagnant. However, even taking this broader view the basic distinction stated at the beginning of this paragraph still stands, namely that while many Norwegian fjords have no oxygen and do have hydrogen sulphide in their deep waters, this condition is uncommon in British Columbia, both in the mainland inlets as described above and, as other investigations have shown, in those in the large islands off the coast.

In discussing the causes of ventilation or lack of it in the Norwegian fjords studied, Strøm mentions several factors. He stresses (1936, p. 11) the effect of offshore winds in the spring carrying away the surface layer which induces an inward flow of subsurface saline water. He also refers to the effect of the fresh water, stating (*ibid.*, p. 58): "Freshwater supplies are of course essential to get more or less permanent density differences between surface and deep, but the degree of stagnation has nothing to do with the volumes of freshwater at the surface. Though very great freshwater supplies preserve deep waters against complete renewals, they cause a certain degree of partial ventilation". These two statements appear to be contradictory. The present writer is of the opinion, contrary to Strøm, that in bodies of water such as the British Columbia inlets and presumably the Norwegian fjords the distribution of subsurface water properties including the degree of stagnation *is* in large measure determined by the fresh water runoff into them. The effect of the fresh water runoff is to drive the estuarine circulation which promotes a renewal of the subsurface waters in the manner described by Tully (1949) and Pritchard (1952) subsequent to the publication of Strøm's work.

The influence of the fresh water runoff then is twofold. In the first place it determines the surface salinity values, decreasing them most in inlets where the runoff is large and giving rise to seasonal variations of surface salinity with a minimum in summer. The surface low salinity layer is 2 to 10 m thick, the salinity value ranging from 2 to 20‰ in summer. By about 20 m depth the salinity even in large-runoff inlets reaches 90 to 95‰ of the deep water value. In the inlets with small runoff the homogeneous surface layer is generally inconspicuous or absent. The temperature structure in the surface layer is influenced by the runoff to the extent that surface values in the large-runoff inlets are low, even in summer, because of the glacial or snowfield origin of the river water. In addition the very strong halocline is accompanied by a strong thermocline. Estimates which have been made of the vertical eddy mixing coefficients for heat and for salt in the upper 200 m indicate that the former is the larger, and seasonal variations of temperature penetrate to a greater depth than do those of salinity. The temperature minimum which is evident in many inlets is believed to be the result of late winter cooling which penetrates to 75 to 100 m although seasonal salinity variations are not noticeable much below 50 m.

The second influence of the fresh water runoff is in promoting the estuarine circulation. The river runoff into the head of an inlet gives rise to a surface outflow which picks up and carries out some of the underlying saline water. In

consequence of this there is a compensatory inflow below the surface layer of saline water from outside. There is evidence in the distribution of subsurface properties of the water in the inlets that the estuarine circulation is stronger in the inlets with large river runoff than in those with smaller runoff. Therefore the deep water characteristics are determined by the river runoff at the surface.

The distribution of dissolved oxygen shows greater variations between inlets than does the temperature, and some of these can be attributed to differences in river runoff. In the inlets with large runoff the surface layers are generally saturated or nearly so with 5 to 8 ml/l. Then, neglecting certain maxima and minima in the upper few tens of metres, the oxygen content decreases at greater depths to 2 to 4 ml/l. This is the general situation in inlets with large runoff. The inlets with small runoff on the other hand have a greater *range* of dissolved oxygen values at any given depth than do the large-runoff inlets. In the surface layers supersaturation is fairly common with values up to 11 ml/l, while in the deep waters the oxygen content is often lower than in the large-runoff inlets at 1 to 3 ml/l. It seems reasonable to suggest that the higher surface values in the low-runoff inlets are associated with the higher salinities which are conducive to greater phytoplankton growth and consequent photosynthetic production of oxygen, together with the slower net seaward movement of the surface layer which permits the phytoplankton populations to develop without being swept out of the inlet. In the deeper water there is a lesser inflow of saline and oxygenated water from outside because of the smaller surface outflow, and therefore the deeper water becomes more depleted of oxygen.

As examples of these last suggestions one may take Bute and Jervis which are geographically close, generally similar in depth and shape, open on to the same body of water in the Strait of Georgia, but show marked differences in some aspects of water structure. The deep water oxygen content in Jervis, particularly near the head, is markedly less than in Bute although the inlet is more directly connected with the Strait of Georgia and has a deeper sill. The chief difference between these inlets is that Jervis has less than 40% as much river runoff as Bute, and only one-quarter of this comes in at the head whereas in Bute three-quarters of the total enters at the head. The flushing effect of the large runoff into the head of Bute is expected to be greater on the whole of the inlet length than that of the smaller runoff distributed along the length of Jervis.

Another example is given by Belize and Seymour which have a common outlet to the sea, but the lower oxygen values in Belize are considered to be a consequence of lower runoff into that inlet. In addition, in Belize itself the main runoff comes in from the side about 8 miles from the head. The reach of the inlet between this junction and the head shows the lowest oxygen values in the length of the inlet and some of the lowest in any of the mainland coast inlets.

Although it is outside the area covered by this paper, Saanich Inlet provides an extreme example on the British Columbia coast of an inlet with small runoff. It does have water with H_2S in its deepest basin. This inlet has a relatively deep sill but an almost complete lack of river runoff into the head. As a result the estuarine circulation is slight and consequently there is stagnation. It is

possible that in the future somewhat more river water may flow into the head of this inlet through diversion and it will be interesting to observe if the extent of stagnation is reduced as a result.

It is remarked that several inlets show a different dissolved oxygen structure with a minimum at mid-depth rather than at the bottom. These are certain of the low-runoff inlets such as Belize and Sechelt. Thompson and Barkey's (1938) suggestion that this is due to reduction in contact with the bottom at mid-depth is questioned. The alternative suggestion is presented that the low runoff, by causing only a slight estuarine circulation, is the main cause of the mid-depth minimum.

In considering the vertical distribution of water properties, particularly in the large-runoff inlets, the fact that upward mixing into the saline zone occurs to a much greater extent than downward mixing, at least until the stability decreases near the inlet mouth, is a well known but not adequately explained feature of the inlet waters. At the same time there is evidence in the inlets with shallow sills that downward mixing does occur to a significant extent even in low-runoff inlets.

In examining the distribution with depth of water properties the possible influence of internal waves which appear to be common must be borne in mind.

10. ACKNOWLEDGMENT

The author wishes to acknowledge assistance from many sources. The Fisheries Research Board of Canada through Dr J. P. Tully of its Pacific Oceanographic Group, Nanaimo, B.C., loaned equipment for the early cruises and provided summer appointments. The Royal Canadian Navy through the Pacific Naval Laboratory, Esquimalt, B.C., made available the oceanographic research vessels C.N.A.V. *Ehkoli*, H.M.C.S. *Cedarwood* and C.N.A.V. *Whitethroat*, and the officers and crews of these vessels contributed materially to the progress of the work.

The greater part of the work reported here was carried out with the assistance of research grants from the National Research Council of Canada, while the work on current measurements and on turbidity described elsewhere and referred to here briefly was supported by the Defence Research Board of Canada under Grants Number 9520-05 and 9520-15.

The Canadian Hydrographic Service, Victoria, B.C., of the Department of Mines and Technical Surveys has been generous in permitting access to detailed field sheets of their surveys.

Finally, while the author directed the field work and took part in most of the cruises the greater part of the field observation and subsequent reduction of data was carried out by student assistants associated with the Institute of Oceanography, University of British Columbia. Reference is made to many of these assistants as authors of papers on specific investigations. Among others

are L. Regan, H. Wilke, T. H. Killam who also prepared the Figures, and G. S. Pond who assisted with data analysis.

For the generous assistance provided by all these organizations and individuals the author wishes to express his sincere thanks.

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On the Chemical Composition of Eleven Species of Marine Phytoplankters¹

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ABSTRACT

Eleven species of marine planktonic representatives of the Chlorophyceae, Chrysophyceae, Bacillariophyceae, Dinophyceae and Myxophyceae have been analyzed for their chemical composition. All species were grown under similar physical and chemical conditions and cells were analyzed during the exponential phase of growth. Chemical analyses consisted of a proximate analysis of each species for ash, protein, carbohydrate and lipid, and an analysis for carbon, silicon and phosphorus, as well as quantitative determinations of the monosaccharides and amino acids in hydrolysates of whole cells. The principal finding of this report is that marine phytoplankton have very similar organic composition when grown under similar physical and chemical conditions, regardless of the size of the organism or the class to which it belongs.

INTRODUCTION

THERE IS a general scarcity of information on the chemical composition of marine phytoplankton. Analyses of natural crops and cells in pure culture (see reviews by Vinogradov, 1953; Strickland, 1960) have been performed on organisms grown under a variety of conditions and using different techniques for the estimation of their composition. Consequently there appears to be no comparative analysis of the different groups of algae which may contribute to a marine phytoplankton crop. In the following presentation an attempt has been made to analyze several representatives of different classes of marine phytoplankton, grown under very similar chemical and physical conditions, and employing standardized techniques for the chemical analyses.

The analytical techniques used are those which have been employed by our laboratory for the measurement of phytoplankton crops *in situ*, and as such are designed for shipboard as well as land-based laboratories. Most of the techniques have been described previously (Strickland and Parsons, 1960). Methods for the quantitative estimation of individual monosaccharides and amino acids, also for some of the other analyses, will be described in outline.

It should be emphasized that the composition of the algal cells reported here applies to vigorously growing cells in the exponential phase of growth, and results would have been different if the cells had been grown under conditions of nutrient deficiency or different conditions of light intensity and temperature. This is well illustrated by work on *Chlorella* by Spoehr and Milner (1949).

¹Received for publication May 15, 1961.

MATERIALS AND METHODS

ALGAL SPECIES

The eleven species employed in this investigation were two members of the Chlorophyceae, *Tetraselmis maculata* and *Dunaliella salina*; two Chrysophyceae, *Monochrysis lutheri* and the coccolithophore *Syracosphaera carterae*; four Bacillariophyceae, *Skeletonema costatum*, *Coscinodiscus* sp., *Chaetoceros* sp. and *Phaeodactylum tricornerutum*; two Dinophyceae, *Exuviella* sp. and *Amphidinium carteri*; and a representative of the Myxophyceae, *Agmenellum quadruplicatum*.

All the cultures were unialgal but not bacteria free. The presence of bacteria during the exponential phase of growth was not apparent and their contribution to the biomass of harvested algal cells was considered insignificant.

MEDIA

Two media were employed for the growth of the phytoplankton cells. The first was ASP 2 as described by Provasoli *et al.* (1957). The second was a medium very similar to ASP 2, but containing a concentration of magnesium, calcium, potassium, borate and bicarbonate ions representative of the concentration of these ions found in sea water. The composition of the latter medium was as follows:

At a salinity of 35‰, a litre of the medium contained 24 g NaCl, 10.9 g MgCl₂·6H₂O, 4 g Na₂SO₄, 0.68 g KCl, 1.5 g CaCl₂·2H₂O, 0.195 g NaHCO₃ and 0.026 g H₃BO₃. To obtain an artificial sea water of a salinity of 25‰, 1.0 volume of this solution was diluted to 1.4 volumes with distilled water. A dilution to 1.06 volumes was made to obtain a salinity of 33‰. All media contained 500 µg-atom N/l as KNO₃ and 50 µg-atom P/l as KH₂PO₄. Trace metals and vitamins were added in the same amount as employed in the ASP 2 medium. Silicon was provided to all media at a concentration of 200 µg-atom Si/l with the exception of the media for the growth of diatoms, where it was provided at a concentration of 1000 µg-atom/l. The silicon was added as a solution of sodium metasilicate and adjusted to pH 8 by the simultaneous addition of HCl.

The choice of the ASP 2 medium for the growth of *Monochrysis lutheri* and *Tetraselmis maculata* was made before the second medium was developed. It was later found that these two organisms grew equally well on the second medium at a salinity of 25‰. *Coscinodiscus* sp., *Skeletonema costatum*, *Chaetoceros* sp., *Phaeodactylum tricornerutum* and *Agmenellum quadruplicatum* were all grown on the second medium described above at a salinity adjusted to 25‰. *Dunaliella salina* and *Syracosphaera carterae* were grown on the same medium adjusted to a salinity of 35‰, and the two dinoflagellates, *Amphidinium carteri* and *Exuviella* sp., on the same medium adjusted to a salinity of 33‰.

CULTURE CONDITIONS

All cultures were grown in 20-l glass bottles under continuous illumination from cool white fluorescent lamps giving an illumination of ca. 0.04 cal/cm²/min. Cultures were stirred and aerated with a stream of filtered air and the temperature was adjusted to 18 ± 2°C with a plastic cooling coil inserted into the medium.

The growth constants shown in Table I for the various algal species were obtained from the slope of the plot of $\log_{10} [\text{Chlorophyll}] a$ against time in hours. Algal cells were harvested at different times depending on the growth rate of the species, but in all cases this was during the exponential phase of growth.

NUMBER, VOLUME AND DRY WEIGHT OF CELLS

NUMBER OF CELLS. Determined using a haemocytometer. The diatom *Coscinodiscus* sp. was too large to be determined by this method and counts were made on settled samples using an inverted biological microscope.

CELL VOLUMES. Determined by direct measurement using a micrometer attachment to the ocular lens of a microscope. Volumes were approximated from the measurements using the closest-fitting geometrical form.

DRY WEIGHT. Determined by filtering a known volume of the medium containing the algal cells onto a Millipore Type AA filter that had been previously washed with distilled water, dried and weighed. The cells were rinsed with isotonic ammonium formate to remove any sodium chloride adhering to the Millipore filter, and dried for 2 hours at 105°C at which temperature any residual formate was volatilized. No measure was made of the amount of moisture that may have been retained after heating at 105°C.

CHEMICAL METHODS

The methods for the determination of protein, carbohydrate, crude fibre, hexosamine, fat, plant pigments, total oxidizable carbon and particulate phosphorus have been described in detail in Bulletin No. 125 of the Fisheries Research Board of Canada (Strickland and Parsons, 1960). The following standards were employed for the determination of the various metabolites:

Protein was estimated by direct Kjeldahl nitrogen determination using ammonium sulphate as a standard and multiplying by the factor 6.25 to give protein. A second method employed for the estimation of protein, using 2,5-hexanedione reagent, was standardized with casein. Carbohydrate, crude fibre and oxidizable carbon estimations were standardized using glucose. Stearic acid was employed as a standard for fat determinations. The method employed for hexosamine determination was that described in Bulletin No. 125 for the estimation of chitin using glucosamine as a standard.

Methods not reported in Bulletin No. 125 are described below:

ASH. Determined on a sample of algal cells dried at 105°C to constant weight and ashed in a muffle furnace at 550°C to constant weight.

SILICON. Determined as silicate after fusion of a weighed sample of dried cells with sodium carbonate. The melt was dissolved in water and the silicate determined colorimetrically with ammonium molybdate.

SUGARS. Individual monosaccharides were determined by chromatographic separation after hydrolysis of a whole plant with sulphuric acid. The technique followed was that described by Wilson (1959) with the modification that the paper chromatography was carried out at 38 to 39°C which resulted in a better

separation of the individual sugars. The solvent employed was butanol : pyridine : water (6 : 4 : 3) and the spots were developed with aniline hydrogen phthalate. The quantity of the individual carbohydrates was determined after elution of the spots and the optical density of the eluate was measured with a Beckman DU spectrophotometer at wavelengths of 390 $m\mu$ for hexoses and methyl pentoses, and 360 $m\mu$ for pentoses. Hexuronic acids were not determined quantitatively and the presence of several minor unidentified sugars was recorded. For confirmation of the identity of certain sugars a second chromatographic solvent, phenol saturated with water, was employed. Use was made also of the orcinol reagent (1% orcinol, 15% trichloroacetic acid in water-saturated butanol) for the detection of ketose sugars on chromatograms.

AMINO ACIDS. Determined using modifications of the techniques described by Consden *et al.* (1944) and Dent (1948). After acid hydrolysis of the plant cells the amino acids were separated by two-dimensional paper chromatography using water-saturated phenol for the first separation and 1 : 1 mixture of 2,4-lutidine and 2,4,6-collidine saturated with water for the second separation. The amino acids were developed with ninhydrin and the individual spots eluted from the paper and compared spectrophotometrically at a wavelength of 570 $m\mu$ with simultaneously run standards of known concentration of natural (L)-amino acids. Leucine, isoleucine and methionine were estimated as one fraction and the presence of minor quantities of some amino acids was noted but not quantitatively determined.

RESULTS AND DISCUSSION

Table I shows the size relations of the algal species to their growth rates.

TABLE I. Cell volumes and growth constants of algal species.

Species	Approximate cell volume	Number of cells per 100 mg dry weight	Growth constant (base 10)	Time required for one cell division
	μ^3		$hour^{-1}$	hours
CHLOROPHYCEAE				
<i>Tetraselmis maculata</i>	310	4.4×10^8	0.039	8
<i>Dunaliella salina</i>	400	7.6×10^8	0.021	14
CHRYSTOPHYCEAE				
<i>Monochrysis lutheri</i>	28	2.9×10^9	0.016	19
<i>Syracosphaera carterae</i>	1,760	2.1×10^8	0.015	20
BACILLARIOPHYCEAE				
<i>Chaetoceros</i> sp.	650	4.4×10^8	0.018	17
<i>Skeletonema costatum</i>	1,390	1.5×10^8	0.023	13
<i>Coscinodiscus</i> sp.	3,420,000	1.4×10^5	0.0083	36
<i>Phaeodactylum tricornutum</i>	120	4.6×10^9	0.013	23
DINOPHYCEAE				
<i>Amphidinium carteri</i>	740	4.0×10^8	0.034	9
<i>Exuviella</i> sp.	780	3.8×10^8	0.0093	33
MYXOPHYCEAE				
<i>Agmenellum quadruplicatum</i>	1.5	1.2×10^{11}	0.020	15

The second column of data gives the number of cells contributing to 100 mg of dry weight. It may be noted that cells of the *Coscinodiscus* sp. had approximately a thousand times the volume of those of the next largest organisms and that they grew at the slowest rate. The sizes of the other organisms vary over a further thousandfold range in cell volume with no obvious correlation between the size of the cell and the growth constant or between pigment content (Table II) and growth constant. This is not unexpected, as the standard growth conditions are not necessarily equally effective for all species.

TABLE II. Proximate analysis of algal cells.

Species	Metabolites (percentage dry weight of cells)					
	Protein*	Carbohydrate	Fat	Total pigment**	Ash	Total
CHLOROPHYCEAE						
<i>Tetraselmis maculata</i>	52	15.0	2.9	2.1	23.8	96
<i>Dunaliella salina</i>	57	31.6	6.4	3.0	7.6	106
CHRYSTOPHYCEAE						
<i>Monochrysis lutheri</i>	49	31.4	11.6	0.8	6.4	99
<i>Syracosphaera carterae</i>	56	17.8	4.6	1.1	36.5	116
BACILLARIOPHYCEAE						
<i>Chaetoceros</i> sp.	35	6.6	6.9	1.5	28.0	78
<i>Skeletonema costatum</i>	37	20.8	4.7	1.8	39.0	103
<i>Coscinodiscus</i> sp.	17	4.1	1.8	0.5	57.0	81
<i>Phaeodactylum tricornutum</i>	33	24.0	6.6	2.9	7.6	73
DYNOPHYCEAE						
<i>Amphidinium carteri</i>	28	30.5	18.0	2.4	14.1	93
<i>Exuviella</i> sp.	31	37.0	15.0	1.1	8.3	92
MYXOPHYCEAE						
<i>Agmenellum quadruplicatum</i>	36	31.5	12.8	1.5	10.7	93

*Nitrogen $\times 6.25$.

**Chlorophylls and carotenoids (sum of mg and MSPU/100 mg dry weight).

Table II shows the proximate analyses of the algal species studied. It may be seen that, with the exception of the two dinoflagellates, protein was the principal organic constituent of the algal cells. In the two dinoflagellates carbohydrate exceeded protein. The chief storage product of the algal cells was carbohydrate in every case except *Chaetoceros* sp. which contained slightly more fat than carbohydrate. The relatively high values for the fat content of the two dinoflagellates are in contrast with other species with the exception of *Monochrysis lutheri* and *Agmenellum quadruplicatum*. Large amounts of ash were found in the diatoms and the coccolithophore, *Syracosphaera carterae*, as was to be expected from previous reports (see review by Vinogradov, 1953). The ash of *Syracosphaera carterae* was approximately 24% calcium carbonate although the number of coccoliths on this organism has been found to vary under different growth conditions from a very heavy coating to a complete disappearance. The surprisingly high ash of *Tetraselmis maculata* was found to be mostly chloride.

The percentages of the different metabolites contributing to the total dry weight of the cells reported in the last column of Table II show some deviation

from a recovery of 100%. Many of the results reported for the analysis of phytoplankton have been obtained by analyzing certain metabolites and calculating at least one component by difference to obtain 100% recovery (e.g. Ketchum and Redfield, 1949). The results reported here show that certain cell constituents were not estimated in terms of the major metabolites reported. In this respect Lewin *et al.* (1958) showed that 12% of *Phaeodactylum tricornutum* was neither protein, lipid, carbohydrate or ash. In a number of the species reported in Table II the percentage recovery is greater than 100%. This may be attributed to the use of average constants for the conversion of biological values. There is no certainty, for example, that the commonly accepted factor 6.25 for the conversion of assayed nitrogen to protein is applicable in every case.

There is little information on which to base interpretation of the nutritional significance of the results in Table II. *Monochrysis lutheri* has been found by Davis and Guillard (1958) to be one of the best foods for oyster larvae. Shiraishi and Provasoli (1959) have reported that *Monochrysis lutheri* was the only organisms of a number tested that would support indefinite growth of the crustacean *Tigriopus japonicus*. One may surmise that the *Monochrysis* cultures fed in both the above experiments were in an exponential growth phase in order to continually produce enough food for the animal populations. It is reasonable to suggest, therefore, that on the basis of the proximate analysis alone, a protein, carbohydrate and fat ratio of approximately 4 : 3 : 1 is suitable for zooplankton nutrition.

Table III shows the carbon content of the species analyzed and the amount

TABLE III. Organic and inorganic composition of algal cells.

Species	Oxidizable carbon (a)	Carbon (by combustion)* (b)	Hydrogen*	Silicon (Si)	Phosphorus (P)	Ratio (b)/(a)
percentage dry weight of cells						
CHLOROPHYCEAE						
<i>Tetraselmis maculata</i>	36.8	35.1	5.4	1.2	3.3	0.95
<i>Dunaliella salina</i>	39.6	45.4	6.3	0.2	3.3	1.15
CHRYSTOPHYCEAE						
<i>Monochrysis lutheri</i>	53.2	44.6	6.6	1.6	3.0	0.84
<i>Syracosphaera carterae</i>	39.6	35.2	3.2	0.2	1.2	0.88
BACILLARIOPHYCEAE						
<i>Chaetoceros</i> sp.	31.0	(-)	(-)	(-)	1.5	(-)
<i>Skeletonema costatum</i>	26.0	31.3	4.4	14.3	1.7	1.20
<i>Coscinodiscus</i> sp.	15.9	18.8	2.9	22.1	0.4	1.18
<i>Phaeodactylum tricornutum</i>	37.5	49.5	6.7	0.3	2.0	1.32
DINOPHYCEAE						
<i>Amphidinium carteri</i>	40.7	47.1	6.7	<0.05	1.1	1.16
<i>Exuviella</i> sp.	44.5	47.4	6.5	0.2	1.3	1.06
MYXOPHYCEAE						
<i>Agmenellum quadruplicatum</i>	42.0	44.9	6.3	1.3	1.4	1.06
Mean carbon ratio:						1.08 ± 0.12

(-)-Samples not analyzed.

*Samples analyzed by Weiler and Strauss, Oxford, England.

of silicon and phosphorus in each species. A comparison has been made between the carbon content of the cells as determined by oxidation with dichromate, and by the classical method of direct combustion. The ratios of the results obtained by the two methods are reported in the last column of the Table. The mean of these ratios agrees with that of El Wakeel and Riley (1957) who suggested the factor of 1.05 for the conversion of dichromate-oxidizable carbon to true carbon in the estimation of the organic content of phytoplankton. High results are obtained by dichromate oxidation in the presence of fats (Johnson, 1949) or other compounds at a higher state of reduction than glucose. Low values may be due to incomplete oxidation by dichromate or to the volatilization of certain compounds during the phosphoric acid treatment employed to remove extraneous chloride (Strickland and Parsons, 1960).

From the values for silicon and phosphorus in Table III it may be seen that the diatoms are the only class of organisms to contain a substantial amount of silicon. The presence of different amounts of silicon in all the other species is of interest in view of the ubiquity of silicon in terrestrial plants and animals (King and Belt, 1938; King *et al.*, 1933; Parry and Smithson, 1957). The phosphorus contents of the cells analyzed were found to be higher than those generally reported in the literature (see review by Strickland, 1960) and these values have been discussed in terms of the nitrogen-to-phosphorus ratios in Table VII.

Table IV presents a comparison between two different methods for the estimation of algal protein. The advantage of the 2,5-hexanedione reagent (Strickland and Parsons, 1960) for the colorimetric estimation of protein is that the method

TABLE IV. Comparison of results of two methods for estimation of proteins.

Species	Colorimetric method (a)	Nitrogen $\times$ 6.25 (b)	Ratio (b)/(a)
<i>percentage dry weight of cells</i>			
CHLOROPHYCEAE			
<i>Tetraselmis maculata</i>	72	52	0.72
<i>Dunaliella salina</i>	68	57	0.84
CHRYSTOPHYCEAE			
<i>Monochrysis lutheri</i>	49	49	1.00
<i>Syracosphaera carterae</i>	53	56	1.06
BACILLARIOPHYCEAE			
<i>Skeletonema costatum</i>	47	37	0.79
<i>Coscinodiscus</i> sp.	18	17	0.94
<i>Phaeodactylum tricornutum</i>	93	33	0.35
DINOPHYCEAE			
<i>Amphidinium carteri</i>	53	28	0.53
<i>Exuviella</i> sp.	36	31	0.86
MYXOPHYCEAE			
<i>Agmenellum quadruplicatum</i>	64	36	0.56
		Mean ratio:	0.77

is applicable under shipboard conditions where the use of fuming sulphuric acid, employed in the Kjeldahl nitrogen determination, is to be avoided. The other reason for employing a second measure of phytoplankton protein is that there appears to be a discrepancy in the determination of protein by the Kjeldahl method. In our own experiments (McAllister *et al.*, 1961) poor agreement between nitrate disappearing and protein being formed during a natural phytoplankton bloom has been reported. Similar discrepancies have been reported by Yentsch and Vaccaro (1959) in the analysis of *Phaeodactylum tricornutum* and by Krey (1958) in studies on natural phytoplankton populations.

The results in Table IV show that the algal species generally gave higher protein values with the 2,5-hexanedione reagent than by total Kjeldahl nitrogen determination. Keeler (1959) investigated the amino acids which react with the 2,5-hexanedione reagent. His results and our determinations of the amino acid composition of the algal species (Table VI) do not explain the variability shown in Table IV for the amount of protein estimated by the colorimetric method. It would appear that nitrogen compounds other than amino acids were present in appreciable amounts.

Table V shows the acid- and alkali-insoluble carbohydrate (crude fibre) as a percentage of the total carbohydrate, also the principal monosaccharides found in hydrolysates of the different algal species as a percentage of the dry weight of algae. The amount of crude fibre found in the different species may be interpreted as indicating the amount of carbohydrate that is employed by the cell for structural support (i.e. cell wall material) as opposed to the amount of carbohydrate stored within the cell. *Tetraselmis maculata*, *Exuviella* sp., *Agmenellum quadruplicatum*, *Coscinodiscus* sp. and *Chaetoceros* sp. were all found to have crude fibre contents greater than 10% of the total carbohydrate. The first three organisms just named were also found to be difficult to extract with 90% acetone for pigment analysis. It may be surmised that these organisms have relatively tough carbohydrate cell walls. The presence of large amounts of crude fibre in two of the four Bacillariophyceae is less readily explained. Diatoms are known to contain carbohydrate associated with the silica of the frustules (see review by Fogg, 1953). It seems reasonable to suggest that the amount of crude fibre associated with the species of *Coscinodiscus* and *Chaetoceros* was due to the relatively large size of the former and the elaborate structure of the latter compared, for example, with *Skeletonema costatum*. In all the other species studied the crude fibre was 10% or less of the total carbohydrate. In contrast, the crude fibre content of sea water has been found to reach 80% of the total carbohydrate when much detritus is present. It appears, therefore, that the level of crude fibre affords a measure of the level of particulate detritus in sea water.

Glucose, galactose and ribose were present in all the species analyzed, while hexuronic acids were detected in all species except the dinoflagellates (Table V). Glucose was always the predominant sugar. The amount of galactose present was variable. Although hexuronic acids were not measured quantitatively on the chromatograms, a measure of their relative amount was obtained using dichromatic

TABLE V. Carbohydrate composition of the algal cells.

Species	Crude fibre (percentage of total carbohydrate)	Principal sugars (percentage dry weight of cells)										
		Glucose	Galactose	Mannose	Ribose	Xylose	Arabinose	Rhamnose	Fucose	Fructose	Hexosamine	Hexuronic acids
CHLOROPHYCEAE												
<i>Tetraselmis maculata</i>	12.6	11.9	2.3	-	0.95	-	-	-	-	-	-	+
<i>Dunaliella salina</i>	9.8	17.2	11.8	-	1.7	-	-	-	-	-	-	+
CHRYSTOPHYCEAE												
<i>Monochrysis lutheri</i>	3.6	22.1	4.4	-	1.3	3.5	-	-	-	-	-	+
<i>Syracosphaera carterae</i>	1.7	9.2	7.1	-	1.5	0.8	1.9	-	-	-	-	+
BACILLARIOPHYCEAE												
<i>Chaetoceros</i> sp.	22.8	3.3	1.5	0.79	0.71	0.4	-	2.8	+	-	-	+
<i>Skeletonema costatum</i>	9.6	16.4	1.8	0.87	1.2	-	-	1.0	0.9	-	-	+
<i>Coscinodiscus</i> sp.	29.0	2.1	0.4	0.41	+	-	-	0.7	0.5	-	-	+
<i>Phaeodactylum tricornutum</i>	2.5	10.7	2.7	3.7	0.72	0.7	-	1.5	-	-	-	+
DINOPHYCEAE												
<i>Amphidinium carteri</i>	2.0	19.0	8.4	-	0.9	-	-	+	-	-	-	-
<i>Exuviella</i> sp.	37.0	26.8	8.3	-	+	+	+	+	-	-	-	-
MYXOPHYCEAE												
<i>Agmenellum quadruplicatum</i>	17.4	17.4	3.2	-	1.5	-	-	-	-	3.5	0.3	+

+Sugars detected but not estimated.
 -Sugars not detected.

readings of the colour produced by the anthrone reaction (Strickland and Parsons, 1960). The results of these measurements showed that hexuronic acids were not present in appreciable amounts. Mannose and rhamnose appeared to be present only in the representatives of the Bacillariophyceae, and fucose also may be a characteristic sugar of this class. Although fucose was not detected in *Phaeodactylum tricornutum*, Lewin *et al.* (1958) have reported its presence in this organism. Xylose appears to be a variable constituent of the algae analyzed while arabinose was only found in the coccolithophore *Syracosphaera carterae*, and the dinoflagellate *Exuviella* sp. Fructose and an unidentified hexosamine were only found in *Agmenellum quadruplicatum*. Two unidentified sugars were detected in the coccolithophore and one in *Chaetoceros* sp. These were minor constituents which appeared ahead of pentoses on the chromatograms.

The occurrence of ribose in every species analyzed is probably attributable to the presence of ribonucleic acid, which Jeener (1952) found to be present in *Polytomella caeca* to the extent of 6 to 10% of the protein.

The occurrence of glucose as the principal sugar in every species further justifies the use of the anthrone reaction (which gives a maximum colour with glucose) for the determinations of total particulate carbohydrate *in situ* (Strickland and Parsons, 1960). From metabolic considerations the amount of glucose occurring in each species reported in Table V further assists in evaluating the nutritional importance of the individual species. Thus in *Monochrysis lutheri*, *Tetraselmis maculata*, *Skeletonema costatum*, *Exuviella* sp. and *Agmenellum quadruplicatum* the amount of glucose is 70% or more of the total carbohydrate. When crude fibre is taken into consideration, however, it would appear that only *Monochrysis lutheri* and *Skeletonema costatum* contain carbohydrates which are both readily hydrolysable and nutritionally important. The importance of *Monochrysis lutheri* as a food for zooplankton has already been mentioned (*loc. cit.*). *Skeletonema costatum* appears to be an equally reliable food for many organisms (Nelson, 1947; Barnes, 1956).

Table VI shows the relative distribution of amino-acid nitrogen. The principal amino acids have been expressed as a percentage of the total estimated amino-acid nitrogen. The presence of other amino acids is recorded in the lower half of the Table. The fact that a number of amino acids were not detected on the chromatograms does not necessarily rule out their presence in the hydrolysates. These amino acids may have been minor constituents which were difficult to detect in the presence of the large amounts of major components.

From the results in Table VI it is apparent that algal protein is characterized by large amounts of aspartic and glutamic acids, glycine, alanine and lysine. The results are in general agreement with other reports (see review by Fogg, 1953) with the exception of the amino acid arginine. Some difficulty was encountered in the detection of arginine on the chromatograms and it was decided, therefore, to estimate arginine by the Sakaguchi reaction (Brand and Kassell, 1942). The

TABLE VI. Amino acid composition of the algal cells.

Amino acids	Species										
	<i>Tetraselmis maculata</i>	<i>Dunaliella salina</i>	<i>Monochrysis lutheri</i>	<i>Syracosphaera carterae</i>	<i>Skeletonema costatum</i>	<i>Coscinodiscus</i> sp.	<i>Phaeodactylum tricornutum</i>	<i>Exuviella</i> sp.	<i>Agmenellum quadruplicatum</i>	<i>Amphidinium carteri</i>	
<i>Amino-acid nitrogen as a percentage of the total amino-acid nitrogen</i>											
Aspartic acid	26.0	16.5	25.3	35.5	28.0	15.6	14.8	20.0	17.0	15.4	
Glutamic acid	8.1	13.6	5.9	5.1	13.5	15.6	12.9	13.1	17.7	11.0	
Glycine	11.1	16.8	8.6	11.4	16.5	12.8	15.6	17.6	16.4	21.2	
Alanine	15.0	19.0	26.0	11.4	7.5	13.8	17.0	13.1	15.7	28.5	
Threonine	—	6.3	5.3	5.1	5.0	7.3	8.7	6.0	3.9	+	
Lysine	21.0	12.0	19.6	17.8	+	12.9	7.2	16.6	13.8	+	
Valine	5.1	4.2	3.7	5.1	8.5	7.3	6.4	4.0	2.6	7.1	
Phenylalanine	7.5	4.5	1.5	2.5	8.0	7.3	11.0	3.5	5.2	8.6	
Leucine	}	6.0	6.9	4.0	6.3	13.0	7.3	6.4	6.0	7.9	8.1
Isoleucine											
Methionine											
<i>Occurrence of other amino acids</i>											
Serine	—	+	+	+	+	+	+	+	+	+	
Proline	+	+	+	+	+	—	+	+	+	+	
Tyrosine	—	+	+	+	—	+	—	—	+	+	
Histidine	—	—	—	—	+	—	—	—	+	—	
Arginine*	—	—	—	—	+	—	—	—	—	—	
Cysteic acid	—	—	+	—	—	—	+	—	—	—	
Methionine sulphoxide	—	+	+	+	—	—	—	+	—	+	

+Amino acid detected but not estimated.

—Amino acid not detected.

*See text for additional values.

estimation was carried out on *Exuviella* sp., *Agmenellum quadruplicatum*, *Monochrysis lutheri* and *Phaeodactylum tricornutum*, and gave respective arginine contents of 1.5, 0.9, 1.2 and 1.5% dry weight of algal cells. These results indicate that arginine was one of the principal amino acids in the species investigated, although the possibility that the Sakaguchi reaction was being given by some other mono-substituted guanidine was not investigated.

Among the occurrences of minor amino acids reported in Table VI those of cysteic acid and methionine sulphoxide can be attributed to the formation of these compounds, during the acid hydrolysis, from cysteine (or cystine) and methionine, respectively. The occurrence of tryptophan in the species analyzed has not been investigated due to the destruction of this amino acid during acid hydrolysis.

A comparison of the distribution of the metabolites in the different species is obtained by comparing ratios of the metabolites to organic carbon. Results are shown in Table VII. Such ratios may be interpreted as an evaluation of

TABLE VII. Ratios involving (oxidizable) carbon values.

Species	$\frac{\text{Protein}^*}{\text{C}}$	$\frac{\text{Carbohydrate}}{\text{C}}$	$\frac{\text{Fat}}{\text{C}}$	$\frac{\text{C}}{\text{P}}$	$\frac{\text{C}}{\text{N}}$	$\frac{\text{N}}{\text{P}}(\text{atoms})$
CHLOROPHYCEAE						
<i>Tetraselmis maculata</i>	1.42	0.41	0.07	11	4.4	5.5
<i>Dunaliella salina</i>	1.43	0.80	0.15	12	4.3	6.1
CHRYSTOPHYCEAE						
<i>Monochrysis lutheri</i>	0.94	0.59	0.22	19	6.8	5.8
<i>Syracosphaera carterae</i>	1.41	0.45	0.12	33	4.4	17.4
BACILLARIOPHYCEAE						
<i>Chaetoceros</i> sp.	1.12	0.22	0.21	21	5.5	8.3
<i>Skeletonema costatum</i>	1.38	0.79	0.17	15	4.4	7.7
<i>Coscinodiscus</i> sp.	1.08	0.27	0.11	40	5.9	15.0
<i>Phaeodactylum tricornutum</i>	0.88	0.64	0.17	19	7.0	5.9
DINOPHYCEAE						
<i>Amphidinium carteri</i>	0.69	0.75	0.44	37	9.0	13.2
<i>Exuviella</i> sp.	0.70	0.84	0.34	34	8.9	12.3
MYXOPHYCEAE						
<i>Agmenellum quadruplicatum</i>	0.86	0.75	0.31	30	7.2	10.6

*Nitrogen $\times 6.25$.

the composition of the different species on an ash-free basis. Due to the difficulty involved in determining ash on natural populations it has been found necessary to use a direct estimation of total carbon as a measure of the organic material for *in situ* studies. Thus the ratios of metabolites to carbon represents an important comparison of the type of metabolites produced by different classes of marine phytoplankton grown under similar conditions. It may be seen that these ratios are considerably less variable than the proximate analysis values reported in Table II. Deviations from this generalization are most marked among the two Dinophyceae and *Agmenellum quadruplicatum*.

Considering the diversity of size and evolutionary origin of the species studied it is remarkable to find such a strong similarity in the composition of the species reported in Table VII. The governing factor in the composition of an algal cell appears to be, therefore, the physical and chemical environment in which it is grown (Spoehr and Milner, 1949). A similar conclusion was reached by Ketchum and Redfield (1949) from a less extensive study of five Chlorophyceae and one diatom.

The finding that different species of organisms grown under the same conditions have similar organic composition is of some advantage to *in situ* studies. Thus phytoplankton, which may be easily netted in large quantities, would be expected to have an organic composition similar to that of the nannoplankton in the same environment. The latter organisms are more difficult to obtain but

may constitute the largest fraction of a crop (e.g. McAllister *et al.*, 1960). Therefore, the organic analysis of a natural crop may be performed on the readily collectible net phytoplankton with reasonable certainty that the results are representative of the organic composition of the entire crop growing under the physical and chemical conditions prevailing at the time of collection. If such a determination is made, however, some measure of the total crop in terms of carbon or pigment is necessary in order to provide a quantitative reference basis for the proportions of protein, carbohydrate and fat.

The nitrogen-to-phosphorus ratios reported in Table VII are generally lower than the classical value of 15:1 (on an atom basis) assumed for *in situ* productivity studies. As mentioned in connection with Table III, this appears to be due to high phosphorus values rather than to low nitrogens (see review by Strickland, 1960). From our own studies (McAllister *et al.*, 1961) using a large plastic sphere to follow the growth of a natural population, it was found that during the exponential phase of growth the N/P ratio was at least as low (5 to 6) as some of the values reported in Table VII. It would appear, therefore, that vigorously growing cells in the presence of adequate nutrients may absorb more phosphorus than the N/P ratio of 15:1 predicts.

In Table VIII the ratios of different metabolites to chlorophyll *a* are reported.

TABLE VIII. Ratios involving chlorophyll *a*.

Species	Carbon Chl. <i>a</i>	Carot.* Chl. <i>a</i>	Protein** Chl. <i>a</i>	Carbohydrate Chl. <i>a</i>	Fat Chl. <i>a</i>	N Chl. <i>a</i>	P Chl. <i>a</i>
CHLOROPHYCEAE							
<i>Tetraselmis maculata</i>	32	0.33	46	13	3	7	2.9
<i>Dunaliella salina</i>	19	0.47	26	14	3	4	1.5
CHRYSTOPHYCEAE							
<i>Monochrysis lutheri</i>	97	0.40	90	57	21	14	5.5
<i>Syracospaera carterae</i>	61	0.49	86	27	7	14	1.8
BACILLARIOPHYCEAE							
<i>Chaetoceros</i> sp.	44	0.26	50	10	10	8	2.1
<i>Skeletonema costatum</i>	26	0.28	36	21	5	6	1.7
<i>Coscinodiscus</i> sp.	69	0.31	75	19	8	12	1.7
<i>Phaeodactylum tricornutum</i>	26	0.44	23	17	5	4	1.4
DINOPHYCEAE							
<i>Amphidinium carteri</i>	48	0.59	48	36	21	5	1.4
<i>Exuviella</i> sp.	62	0.47	62	51	21	7	1.8
MYXOPHYCEAE							
<i>Agmenellum quadruplicatum</i>	45	0.56	45	34	14	6	1.5

*Carotenoids expressed in MSP units.
 **Nitrogen $\times$ 6.25.

The amounts of chlorophyll *a* from which these ratios have been obtained were determined at the same time as the other analyses reported here. Complete results of the pigment analyses have been reported by Parsons (1961). In the

estimation of phytoplankton crops *in situ* it is impossible to obtain a direct measure of various metabolites present in the plants, because of the presence of large amounts of detritus in sea water (Parsons and Strickland, 1959; McAllister *et al.*, 1960). Consequently the amount of a plant metabolite must be calculated from a prior knowledge of the ratio between the pigment concentration in the naturally occurring species and the metabolite being measured. Thus Table VIII serves as a guide to the range of values to be expected from the various classes of organisms. These values are in general agreement with average values quoted by Strickland (1960) but one or two individual characteristics of the classes are worthy of note.

The ratio of carbon and protein to chlorophyll *a* (Table VIII) was found to be higher for the two Chrysophyceae than for any of the other groups. Fat and carbohydrate ratios were found to be high for the two Dinophyceae, *Agmenellum quadruplicatum* and the two Chrysophyceae. The representatives of the Bacillariophyceae show considerable variation while the two Chlorophyceae are characterized by the lowest ratios. The ratios of total carotenoids to chlorophyll *a* are remarkably constant throughout the different classes. A similar constancy in the chlorophyll *a*-to-carotenoid ratio has been found to occur in the natural populations of coastal waters throughout the year (Parsons, 1960) but its significance has not been interpreted.

ACKNOWLEDGMENTS

We would like to thank Dr R. R. L. Guillard (Woods Hole Oceanographic Institution), Dr V. L. Loosanoff (Biological Station, Milford), Dr C. Van Baalen (Kitchewan Research Laboratories) and Dr J. R. Stein (University of British Columbia) for cultures of organisms used in these experiments. We would like to thank also Mr A. Bursa (Arctic Unit, Fisheries Research Board, Montreal), Dr J. Stein and Dr E. M. Hulbert (Woods Hole Oceanographic Institution) for the identification of some of the species.

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On the Pigment Composition of Eleven Species of Marine Phytoplankters¹

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ABSTRACT

The amounts of different chlorophylls and carotenoids in eleven representatives of marine phytoplankton have been estimated. Representatives of the Chlorophyceae, Chrysophyceae, Bacillariophyceae, Dinophyceae and Myxophyceae were grown under similar chemical and physical conditions and their pigment content was determined during the exponential phase of growth. Particular attention was paid to the presence of chlorophyll *c* as well as to the identity of certain carotenoids.

IN A PREVIOUS PUBLICATION (Parsons *et al.*, 1961) the chemical composition of eleven species of marine phytoplankton was studied. The results reported here are a continuation of this work with a view to establishing the quantitative and qualitative differences in the phytosynthetic pigments of these principal classes of marine phytoplankton. Considering the marked variation in pigment content of cells grown under different physical and chemical conditions described by previous investigators (Stanbury, 1931; Haskin, 1941; Strain *et al.*, 1944), the same precautions for standardizing growth conditions as described previously (Parsons *et al.*, 1961) were employed in the studies reported here.

MATERIALS AND METHODS

ALGAL SPECIES AND CULTURE CONDITIONS

The unialgal cultures employed in this investigation were two members of the Chlorophyceae, *Tetraselmis maculata* and *Dunaliella salina*; three Chrysophyceae, *Monochrysis lutheri* and the coccolithophores *Syracosphaera carterae* and *Coccolithus huxleyi*; four Bacillariophyceae, *Skeletonema costatum*, *Coscinodiscus* sp., *Chaetoceros* sp. and *Phaeodactylum tricornutum*; two Dinophyceae, *Exuviella* sp. and *Amphidinium carteri*; and a representative of the Myxophyceae, *Agmenellum quadruplicatum*.

The media and growth conditions for the algal cultures were the same as reported previously (Parsons *et al.*, 1961) with the exception of conditions for the growth of *Coccolithus huxleyi*. This organism, which has been used here in connection with studies on chlorophyll *c*, was grown in a medium of 33‰ salinity (Parsons *et al.*, 1961) at a temperature of 16°C and under a light intensity of 0.065 cal/cm²/min from cool white fluorescent bulbs.

¹Received for publication May 15, 1961.

CHEMICAL METHODS

CHLOROPHYLLS AND TOTAL CAROTENOIDS

The method for the determination of chlorophylls *a*, *b* and *c* and the total plant carotenoids was that described by Richards with Thompson (1952), with the spectrophotometric corrections as modified by Strickland and Parsons (1960).

INDIVIDUAL CAROTENOIDS

The amounts of the individual algal carotenoids were determined by a chromatographic technique similar to that described by Strain *et al.* (1944) for the separation of algal pigments on columns of sugar.

Fresh cells were collected on a Millipore AA filter and extracted overnight (16 hours) in 90% acetone in the presence of a small amount of magnesium carbonate. Water was added to the acetone extract and the pigments were transferred to hexane in a separatory funnel. The hexane extract was taken to dryness by blowing with a stream of nitrogen, and the pigments were redissolved by washing with several small (0.5-ml) portions of hexane.

The chromatographic apparatus was obtained as a unit (No. 57824) from Scientific Glass Apparatus Co., Bloomfield, N.J. The column was prepared by the addition of a slurry of starch (Analar, reagent grade) in hexane and packed under pressure (100 cm of water) from a nitrogen cylinder to a height of 20 cm. The sample was applied to the top of the column, under the same pressure at which the column was packed, and washed on with two 10-ml portion of hexane. Approximately 200 ml of hexane was then added to the reservoir at the top of the column, and allowed to percolate through the column under pressure.

With representatives of the Chrysophyceae, Dinophyceae, Myxophyceae and Bacillariophyceae, a single chromatographic separation sufficed to resolve the pigments into their major components. No attempt was made to separate isomers of the different pigments or to resolve the different carotenes. Following the elution of the carotenes with hexane, the eluting solvent was changed to 0.5% *n*-propanol in hexane which removed chlorophyll *a* followed by the xanthophylls. Fucoxanthin, peridinin and an unidentified xanthophyll from *Agmenellum quadruplicatum* moved very slowly with 0.5% *n*-propanol in hexane, and usually were eluted with 2% *n*-propanol in hexane.

With representatives of the Chlorophyceae it was found that the chlorophylls would not separate from two xanthophylls (Fractions II and III in Table II) on elution with 0.5% *n*-propanol in hexane. The combined fraction of chlorophylls and xanthophylls was therefore chromatographed again on starch and eluted with hexane. The xanthophylls which ran ahead of the chlorophylls were cut out of the column and eluted with acetone. Two closely associated xanthophyll bands (Fractions IV(A) and (B) in Table II) which remained behind on the original column after elution with 0.5% *n*-propanol in hexane were similarly eluted with acetone.

Spectra of the various pigments were measured in hexane, also in carbon disulphide and chloroform when their identity was uncertain. Measurements

were made using a Beckman DU spectrophotometer and the pigments identified from absorption spectra reported by a number of authors (Strain *et al.*, 1944; Deuel, 1951; Goodwin, 1955; Dales, 1960). The quantity of carotenoid present in each fraction was estimated from the volume of the effluent and the optical density of the carotenoid at the wavelength of maximum absorption. When the specific absorption coefficient was not known, the specific absorption coefficient for β -carotene was used to calculate the approximate quantity of a pigment (Goodwin, 1955).

PREPARATION OF CHLOROPHYLL *c*

In order to confirm the presence of chlorophyll *c* in certain species a separation of this pigment from most of the carotenoids and chlorophyll *a* was achieved by the following procedure.

Plants were extracted with 90% acetone in the presence of a small amount of magnesium carbonate. An equal volume of water was added to the acetone extract and the aqueous mixture was extracted three times with hexane. The hexane layer was discarded after each extraction. The acetone-water mixture was then extracted once with chloroform and the chloroform evaporated with a stream of nitrogen. The dried residue was taken up in methanol or ether and the spectrum measured on a Beckman DU spectrophotometer.

RESULTS AND DISCUSSION

Table I shows the quantitative distribution of chlorophylls and total carotenoids in the species studied. Chlorophyll *a* was found to be the predominant pigment in all the species studied, except *Amphidinium carteri* in which chlorophyll *c* predominated. Quantitatively, the amount of chlorophyll *a* was quite variable. The two Chrysophyceae have the least chlorophyll *a* of any class,

TABLE I. Chlorophylls and total carotenoids.

Species	Chlorophyll <i>a</i>	Chlorophyll <i>b</i>	Chlorophyll <i>c</i>	Total carotenoids
	—mg or MSPU per 100 mg dry weight—			
CHLOROPHYCEAE				
<i>Tetraselmis maculata</i>	1.14	0.56	0	0.38
<i>Dunaliella salina</i>	2.19	0.50	0	1.02
CHRYSTOPHYCEAE				
<i>Monochrysis lutheri</i>	0.55	0	0.03	0.22
<i>Syracosphaera carterae</i>	0.65	0	0.15	0.32
BACILLARIOPHYCEAE				
<i>Skeletonema costatum</i>	1.00	0	0.56	0.28
<i>Coscinodiscus</i> sp.	0.23	0	0.16	0.07
<i>Phaeodactylum tricornutum</i>	1.44	0	0.87	0.63
<i>Chaetoceros</i> sp.	0.70	0	0.56	0.18
DINOPHYCEAE				
<i>Amphidinium carteri</i>	0.85	0	1.10	0.50
<i>Exuviella</i> sp.	0.72	0	0.06	0.34
MYXOPHYCEAE				
<i>Agmenellum quadruplicatum</i>	0.93	0	0	0.52

while the two Chlorophyceae contain relatively large amounts of chlorophyll *a*. Chlorophyll *b* was only found in the Chlorophyceae, as was to be expected from earlier reports (see review by Strain, 1951).

The large amount of chlorophyll *c* in *Amphidinium carteri* and the presence of chlorophyll *c* in the two representatives of the Chrysophyceae required further investigation in view of the inaccuracy of determining this pigment by the Richards method (Richards with Thompson, 1952). An attempt was made, therefore, to extract the chlorophyll *c* from *Amphidinium carteri*, *Monochrysis lutheri* and *Coccolithus huxleyi*. The last-named organism has been employed in these studies because it has been found in our laboratory (unpublished result) to contain considerably more chlorophyll *c* (ca. 50% of the chlorophyll *a*) than is reported for the two other Chrysophyceae in Table I.

The spectra for chlorophyll *c* in ethyl ether, as extracted from *Amphidinium carteri* and *Coccolithus huxleyi*, are shown in Fig. 1 and 2 respectively. The chlorophyll *c* spectrum from *Amphidinium carteri* appears to be virtually free of chlorophyll *a* and has absorption maxima at 447, 578, and 627 m μ . In methanol, the same pigment gave absorption maxima at 450, 584 and 633 m μ . These values are in good agreement with values reported by Smith and Benitez (1955) for pure chlorophyll *c* in ether and methanol. The absorption minimum for chlorophyll *c* at 500 m μ , reported by those investigators, occurred at 510 m μ

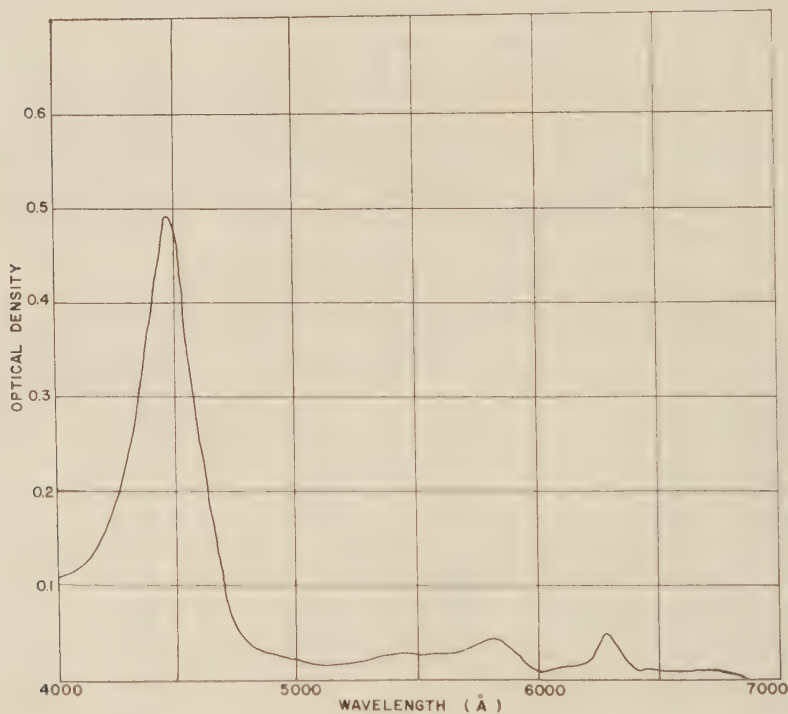


FIG. 1. Spectrum of chlorophyll *c* in ether extracted from *Amphidinium carteri*.

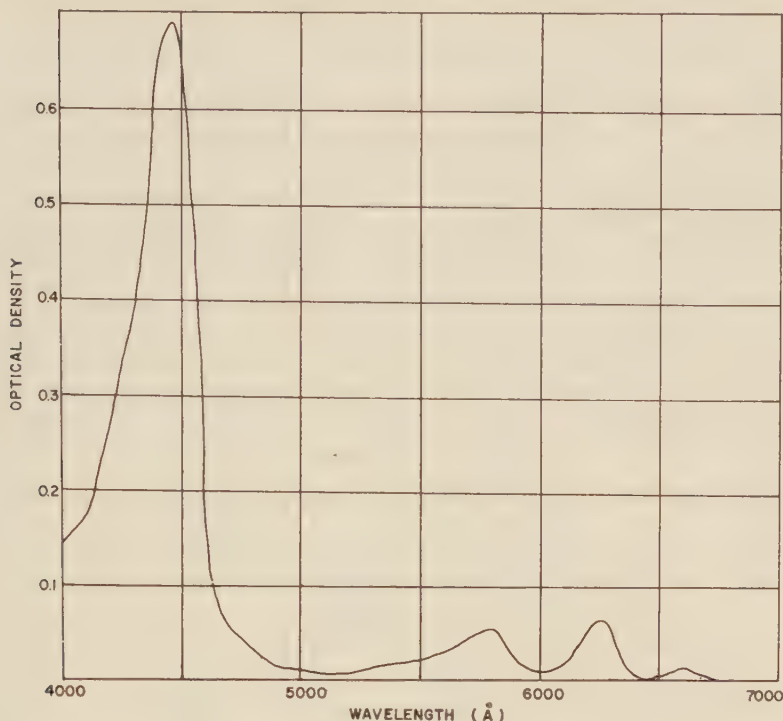


FIG. 2. Spectrum of chlorophyll *c* in ether extracted from *Coccolithus huxleyi*.

in the spectrum shown. This is probably due to contamination with a small amount of a carotenoid. The spectrum for chlorophyll *c* from *Coccolithus huxleyi* (Fig. 2) is similar to that shown for *Amphidinium carteri* having absorption peaks at 447, 578, 627 and 660 $m\mu$. The small peak at 660 $m\mu$ is probably due to contamination with chlorophyll *a* which Smith and Benitez have reported as being difficult to remove completely from chlorophyll *c*. A spectrum similar to that shown for *Coccolithus huxleyi* was obtained with *Monochrysis lutheri*. Dales (1960) has reported that chlorophyll *c* is absent from the Chrysophyceae. In referring to a yellow, water-soluble pigment found in the Chrysophyceae by Gaidukov (1900), Dales concluded that this was a contaminant in the culture preparation. It would appear from the findings presented here that Gaidukov's water-soluble pigment was chlorophyll *c*.

The amount of chlorophyll *c* in *Syracosphaera carterae* and *Monochrysis lutheri* reported in Table I is quite small and could not be detected in a chromatogram. Under certain conditions, however, the amount of chlorophyll *c* in *Monochrysis lutheri* has been found to increase. The increase appears to be associated with a high light intensity, lower temperature and nutrient-deficient cells. The large amount of chlorophyll *c* in *Amphidinium carteri* was confirmed by measuring the amount of chlorophyll *c* obtained after removal of most of the chlorophyll *a* and carotenoids. This value was some 80% of the value found by the Richards

method (Richards with Thompson, 1952), which, considering losses during extraction, is in fairly good agreement.

There are a number of reports (Currie, 1958; Humphrey, 1960; McAllister *et al.*, 1960) showing that amounts of chlorophyll *c* often exceed chlorophyll *a* in plankton samples from ocean waters. In our own studies (McAllister *et al.*, 1960) the principal group of organisms believed to be responsible for the total crop in the Northeast Pacific Ocean are the coccolithophores. The inconsistency between this finding and Dales' (1960) reported absence of chlorophyll *c* in members of the Chrysophyceae now appears to be remedied in part. The largest amount of chlorophyll *c* found by us (*loc. cit.*) to be present in a Chrysophycean, however, was in *Coccolithus huxleyi*. It contained about 50% of the amount of chlorophyll *a* present. This is still less than the values reported from ocean waters and further investigation of high chlorophyll *c* values in the oceans would seem necessary.

Table II shows the amount of the various carotenoids present in the different

TABLE II. Principal carotenoids of the algal cells.

Species	Fractions in order of elution	Wavelength of maximum absorption in hexane			Carotenoid	Amount
		mμ	mμ	mμ		
CHLOROPHYCEAE						
<i>Tetraselmis maculata</i>	I (A)	~428,	452,	480 (β)	Carotenes	0.106
	(B)	~430,	462,	494 (α)		
	II	419,	446,	475	Lutein	0.070
	III	446,	472		Unidentified	0.041
	IV (A)	443,	476		Violoxanthin	0.039
(B)	436,	468		Neoxanthin		
<i>Dunaliella salina</i>	I	~425,	450,	475	Carotenes	0.149
	II	422,	445,	477	Lutein	0.416
	III	442,	470		Unidentified	0.129
	IV	436,	467		Neoxanthin	0.049
CHRYSTOPHYCEAE						
<i>Monochrysis lutheri</i>	I	~425,	450,	474	Carotenes	0.042
	II	447,	477		Diadinoxanthin	0.066
	III	450,	478		Fucoxanthin	0.069
<i>Syracosphaera carterae</i>	I	~425,	450,	480	Carotenes	0.048
	II	447,	476		Diadinoxanthin	0.107
	III	450,	480		Fucoxanthin	0.145
BACILLARIOPHYCEAE						
<i>Skeletonema costatum</i>	I	~425,	450,	479	Carotenes	0.050
	II	448,	477		Diadinoxanthin	0.051
	III	450,	480		Fucoxanthin	0.176
<i>Coscinodiscus</i> sp.	I	~425,	450,	475	Carotenes	0.012
	II	450,	480		Diatoxanthin	0.007
	III	448,	477		Diadinoxanthin	0.010
	IV	450,	480		Fucoxanthin	0.037
<i>Phaeodactylum tricornutum</i>	I	~425,	450,	478	Carotenes	0.059
	II	448,	477		Diadinoxanthin	0.154
	III	450,	480		Fucoxanthin	0.740
DINOPHYCEAE						
<i>Amphidinium carteri</i>	I	~425,	450,	478	Carotenes	0.042
	II	448,	477		Diadinoxanthin	0.129
	III	454,	485		Peridinin	0.258
<i>Exuviella</i> sp.	I	~425,	450,	477	Carotenes	0.025
	II	448,	477		Diadinoxanthin	0.081
	III	454,	485		Peridinin	0.130
MYXOPHYCEAE						
<i>Agmenellum quadriplicatum</i>	I	~425,	450,	478	Carotenes	0.213
	II	450,	479		Antherxanthin	0.162
	III	452,	480		Unidentified	0.033

~Indicates an inflection.

species analyzed. It will be seen that fucoxanthin is the predominant carotenoid of the three Bacillariophyceae, and the two Chrysophyceae. The presence of diadinoxanthin in the Chrysophyceae agrees with results found by Dales (1960). This latter pigment was found during chromatography to run considerably slower than lutein but was inseparable from diadinoxanthin prepared from diatoms. An additional property of this compound was found to be that on treatment with dilute HCl there was a spectral shift in the wavelengths of maximum absorption in hexane from 447 and 477 $m\mu$ to 428 and 456 $m\mu$. This shift of approximately 20 $m\mu$ is characteristic of the isomerization of 5,6-epoxides to 5,8-epoxides (Goodwin, 1955). The HCl derivative of diadinoxanthin ran above diadinoxanthin on the starch column. It was found, in fact, that if *Monochrysis lutheri* was extracted with acetone in the absence of magnesium carbonate then a second band appeared above diadinoxanthin. This was an artifact which did not occur if the cells were extracted in the presence of magnesium carbonate immediately following filtration. Allen *et al.* (1960) have not reported diadinoxanthin in the two representatives of the Chrysophyceae that they studied. However, these authors record several unknown pigments. At least one of these (Fraction D in the *Prymnesium parvum* analysis) appears to be similar to HCl-treated diadinoxanthin.

Diatoxanthin was only estimated in one diatom, *Coscinodiscus* sp. It was detected as running below diadinoxanthin in extracts of *Monochrysis lutheri* and *Phaeodactylum tricornutum* but was not observed at all in *Skeletonema costatum* or in *Syracosphaera carterae*. Its presence in the Bacillariophyceae and Chrysophyceae may be quite variable, however, since in old cultures of *Monochrysis lutheri*, grown under brighter illumination, it has been observed to occur in appreciable amounts. Allen *et al.* (1960) have reported the presence of diatoxanthin in the two Chrysophyceae they analyzed, while Dales (1960) has recorded it as being absent in the eight species studied by him.

In *Dunaliella salina* the predominant carotenoid was lutein while in *Tetraselmis maculata* it was associated with the carotene fraction. In the latter species there appeared to be two distinct carotenes present as determined by measuring the spectrum of the first part of Fraction I as compared with the last part of the fraction. The spectrum of the first part of this fraction (A) was similar to that of β -carotene while the last part (B) was similar to γ -carotene. The last fraction to be eluted from the column (Fraction IV) also was composed of two parts, the first of which (A) was spectroscopically similar to violoxanthin and the last (B) to neoxanthin. The identification of Fraction III reported for the Chlorophyceae is uncertain. The position of this fraction on the starch column would suggest that it was lutein-5,6-epoxide. However, the wavelengths of maximum absorption in carbon disulphide of 475 and 506 $m\mu$ were rather high compared with those reported by Goodwin (1955). In addition, the pigment was stable to treatment with dilute HCl, which indicated that it was not 5,6-epoxide (Deuel, 1951).

In the two dinoflagellates the principal carotenoid was peridinin. Dincoxanthin, reported to occur in dinoflagellates by Strain *et al.* (1944), was not observed. This pigment may have been, however, a minor constituent of these

species which was not detected in the presence of large amounts of the other carotenoids.

The carotenoids reported for the species of Myxophyceae, *Agmenellum quadruplicatum*, are in contrast with those reported to identify this class of organisms. Goodwin (1957) reported that the Myxophyceae are characterized by β -carotene, echinenone, zeaxanthin and myxoxanthophyll. With the exception of β -carotene none of these pigments were found to occur in *Agmenellum quadruplicatum*. The identity of antherxanthin as one of the pigments of *Agmenellum quadruplicatum* has been based on its absorption maxima in chloroform at 460 and 490 $m\mu$ and in carbon disulphide at 480 and 510 $m\mu$. Goodwin (1955) has reported that antherxanthin has absorption maxima at 460.5 and 490.5 $m\mu$ in chloroform and 482 and 510 $m\mu$ in carbon disulphide. On treatment with dilute HCl, the antherxanthin fraction, reported in Table II, showed a shift in the wavelengths of maximum absorption in hexane from 450 and 479 $m\mu$ to 450 and 424 $m\mu$. Antherxanthin is the 5,6-epoxide of zeaxanthin and has been found to show an epoxide shift on treatment with HCl to give the 5,8-epoxide known as mutatoxanthin (Deuel, 1951). Mutatoxanthin has been reported by Deuel to have absorption maxima in petroleum ether at 426 and 456 $m\mu$. While this is not a particularly close fit with the HCl-treated antherxanthin reported above, the HCl treatment was found to cause an eventual disappearance of all absorption maxima above 400 $m\mu$ which may account for the relatively poor agreement with the reported maxima.

The last fraction (Fraction III) to be separated from the *Agmenellum quadruplicatum* has not been identified. No attempt was made to characterize or estimate the phycobilin pigments in this species. On a quantitative basis the results reported here for *Agmenellum quadruplicatum* agree with the finding by Goodwin (1957) who has reported that β -carotene is the predominant carotenoid of the Myxophyceae. There have been other reports (for references see Goodwin, 1957) on the presence of xanthophylls in the Myxophyceae other than echinenone, zeaxanthin and myxoxanthophyll. None of the reported pigments agree with the finding presented here, however, and the only other reported occurrences of antherxanthin have been in the anthers of flowers (Deuel, 1951) and in the echinenoids and asteroids (Fox, 1953).

Recent experiments in this laboratory have shown that the specific absorption coefficient of peridinin is less than half that of β -carotene on which the determination of the former pigment was based. This would increase the amount of peridinin found in the two dinoflagellates by a factor of approximately 2.5. The specific absorption coefficient of chlorophyll *c* employed for the determinations cited above also is in doubt. Recent evidence indicates that the chlorophyll *c* determinations reported here have been overestimated by a factor of approximately 2.

ACKNOWLEDGMENT

The author would like to express his thanks to Mr Wing Wai for technical assistance during the course of these studies.

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Some Oceanographic Features of Juan de Fuca Strait¹

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ABSTRACT

The distribution and structure of dissolved oxygen, salinity, temperature and density, and their seasonal and tidal variations are summarized, and related to the tidal and estuarine mechanisms.

Juan de Fuca Strait is a complex, deep, positive estuary. It is divided into inner and outer parts by a sill extending southward across the channel from Victoria, B.C. The Inner Strait

¹Received for publication May 23, 1961.

is separated from the Strait of Georgia by the San Juan Archipelago. The water structure in the Strait of Georgia is highly stratified due to the shallow brackish upper zone maintained by the Fraser River discharge. This brackish water tends persistently seaward due to the estuarine mechanism. In the passages through the San Juan Archipelago the shallow and deep waters are mixed to near homogeneity by the turbulent tidal flows. In the Inner Strait the stratification is small. Part of this mixed water is fed back into the lower zone of the Strait of Georgia, and part escapes seaward in the upper zone of the outer part of Juan de Fuca Strait, where it overruns the intruding ocean water, creating a new stratification. The ebb flow is stronger than the flood in this upper zone, and the halocline is deepest on the northern side of the strait.

The flood flow, augmented by the deep inflow required by the estuarine mechanism, is strongest in the lower zone. Here the ocean waters advance over the sill during the flood flow, but do not retreat during the ebb flow, which is relatively weak. These ocean waters are incorporated with the mixed waters in the Inner Strait. This mechanism is a tidal pump.

The concentration of fresh water in the upper zone of Juan de Fuca Strait varies from 2 to 6‰ during the year. The amount (depth of fresh water when separated from the ocean water in the system) varies from 1 to 7 m. In this and all other properties there is a gradient from the Strait of Georgia into the Inner Strait. In the Outer Strait there are cross-channel gradients, but none longitudinally.

Throughout the system the density structure is salinity dominated. During the summer the thermocline coincides with the halocline. In winter the waters are isothermal, or the upper waters become slightly colder than the deep waters. Then the stability depends on the salinity structure alone.

The salinity is a linear function of temperature within 0.1°C , except at the surface in summer. The slope of the relation varies with time (season) and location. The relation shows that the waters throughout the system are mixtures of ocean water and brackish water from the Strait of Georgia, and tributary inlets.

INTRODUCTION

JUAN DE FUCA STRAIT (Fig. 1) is the principal approach to the Strait of Georgia and Puget Sound from the sea. Therefore, it was desirable to have an oceanographic investigation to provide complete synoptic charts of the structure, and to establish the mechanics of sea water exchange between the Strait of Georgia and the sea.

GEOGRAPHY AND CLIMATE

GEOGRAPHY

As shown in Fig. 1 Juan de Fuca Strait is a submarine valley extending from the ocean (Cape Flattery) to the channels of the San Juan Archipelago. It is bounded on the north by the low (600-m) Seymour Range on Vancouver Island, and on the south by the high (1800-m) Olympic Range in the State of Washington. The eastern limit borders a low (100-m) coastal plain.

The strait contains two basins (Fig. 2) where depths greater than 100 m (55 fathoms) are found. These are separated by a sill, a cross-channel ridge lying southward from Victoria, B.C., at 60 m (33 fathoms) depth. The "Inner Strait" contains several shallow banks, through which the deepest channel leads into Haro Strait, and lesser channels lead to Rosario Strait and Admiralty Inlet.

The "Outer Strait" deepens gradually to seaward to more than 200 m at Cape Flattery. Beyond the cape (Fig. 1) this valley turns southward at right

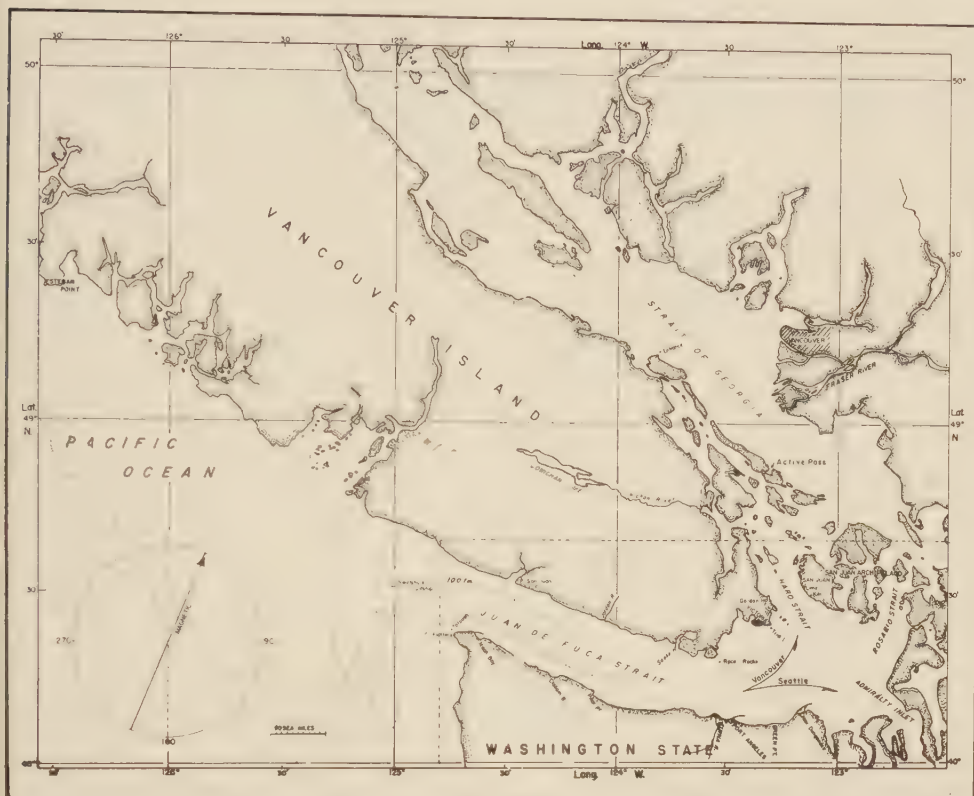


FIG. 1. Juan de Fuca Strait and adjacent sea regions (Chart 3607, Canadian Hydrographic Service, 1952).

angles and cuts through the continental shelf and down the continental slope to the ocean abyss.

CLIMATE

The weather data have been summarized by the Canadian Meteorological Service (1896–1957) and United States Weather Bureau (1953). Some features of the climate have been discussed by Kendrew and Kerr (1955).

AIR TEMPERATURE

The air temperature cycle at any one place in Juan de Fuca Strait is in phase with the air temperature cycle experienced along the whole British Columbia coast, but the range of the cycle varies along and across the channel. Figure 3 shows the annual air temperature cycle at several locations in the area. In the winter, the air at the entrance (Tatoosh Island) is warmer than in the Inner Strait (Port Angeles) by 2°C . In summer this relation is reversed. The eastern extremity (Anacortes) is almost 10°C warmer than Tatoosh Island during July. Across the channel, the air temperature shows a 2°C difference from Jordan River to Clallam Bay.



FIG. 2. Juan de Fuca Strait, showing bottom topography and locations of observations.

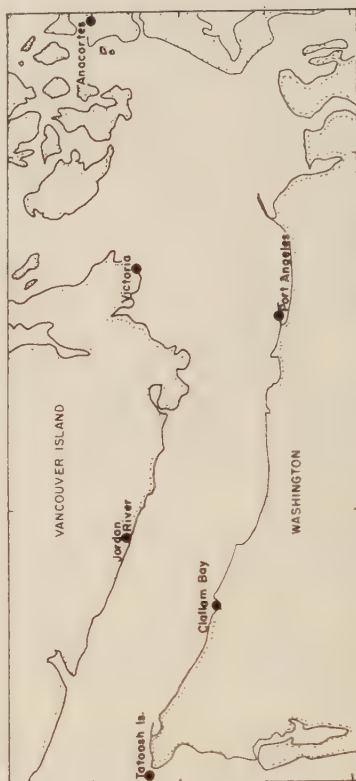
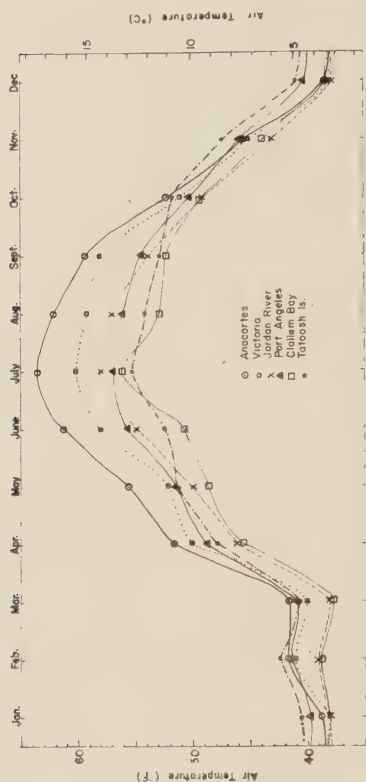


FIG. 3. Air temperatures in Juan de Fuca Strait 1952. Tatoosh Island, Port Angeles, Jordan River, Clallam Bay.

PRECIPITATION AND RUNOFF

The precipitation in Juan de Fuca Strait varies considerably from one end to the other (Fig. 4). The average precipitation at Neah Bay, at the entrance,



FIG. 4. Juan de Fuca drainage area and average annual precipitation.

is 272 cm (107 in) per year; at Port Angeles, 69.5 cm (27.4 in); and in the southern San Juan Islands, 49 cm (19.3 in) per year. It is noteworthy that the precipitation is much greater on the western side of the mountains than on the eastern side.

The drainage area into Juan de Fuca Strait (Fig. 4) includes the surface of the southern part of the Strait of Georgia (Waldichuk, 1957), Puget Sound, and the many smaller seaways. It also includes the islands of the San Juan Archipelago, adjacent islands, the southeastern coastal slopes of Vancouver Island, coastal slopes of the adjacent mainland, and the basin of the Fraser River, which extends inland for 1500 miles (2500 km).

In this area, precipitation varies from 40 to more than 250 cm (15 to 100 in) per year, depending on the location. Generally it is greatest on the western side of the mountains, and decreases from seaward to the interior of British Columbia. In general, the precipitation is greatest in winter and least in late summer (Fig. 5).

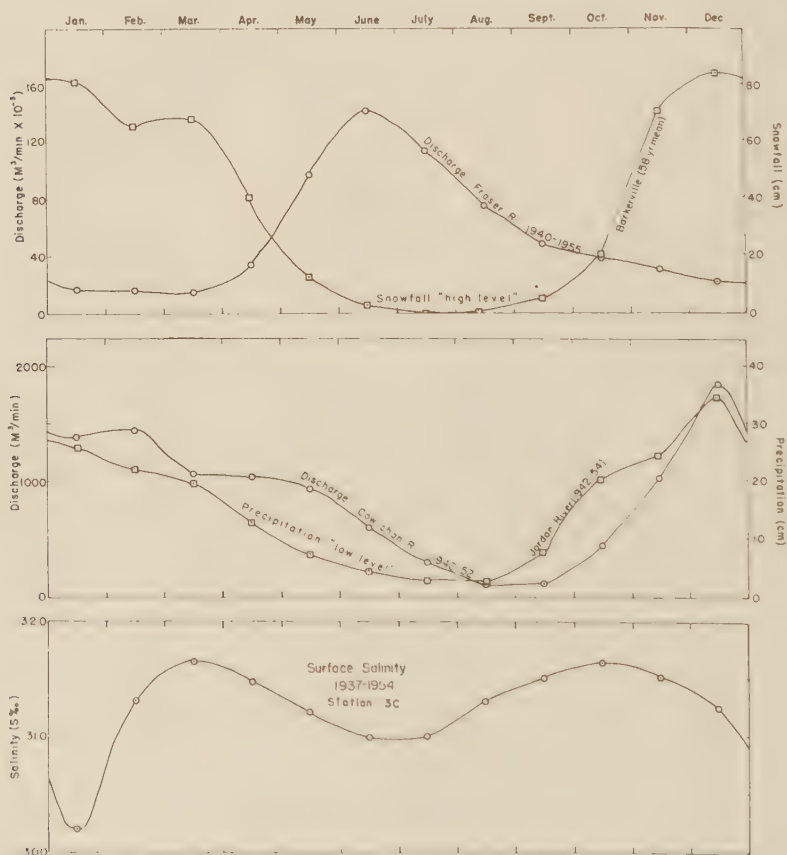


FIG. 5. Features of precipitation and discharge of representative high and low level coastal rivers.

Most of the drainage areas are high mountainous regions where winter snow storage plays a major part in regulating the runoff. The snow cover advances to sea level in January, and retreats to the permanent snow level at about 1500 m (5000 ft) altitude in September. The precipitation is greatest at high levels but drainage does not occur until the spring thaws, so that rivers draining the high levels commence to rise in late March, and reach their maximum discharge in June. This is particularly true of the Fraser River (Fig. 5) (Canadian Water Resources Branch, Annual).

The coastal climate at sea level is mild, and in the winter, when precipitation is greatest, this usually occurs as rain. Even when there is snow, this seldom lies as long as a month (January). The land drainage at low levels near the sea closely follows the precipitation and is greatest in winter. This is illustrated in the discharge of the Cowichan River in the middle diagram of Fig. 5.

The average annual precipitation in the Fraser River basin was compared to the precipitation into the whole drainage basin of the Straits of Georgia and Juan de Fuca. From this study it was deduced that 70 to 75% of the fresh water in the system is supplied by this one river. Undoubtedly the proportion is greater in June and less in January, but it is the principal fresh water source, and all others may be regarded as local.

The rivers discharging into Juan de Fuca Strait from the northern (Canadian) side are generally the "low level" type similar to the Cowichan River (Fig. 5) whose maximum discharge occurs in winter. On the southern side of the strait, the head waters of the rivers are in the high Olympic Mountains where the winter precipitation is stored as snow. The maximum discharge of these rivers occurs in the summer. Thus there are two periods of high runoff; one associated with the melting snow at high levels, and lesser, local maxima in winter associated with the peak of coastal precipitation.

WINDS

The principal winds (Canadian Meteorological Service, 1896-1957) along the ocean coast (Fig. 6) are southeasterly in winter, and northwesterly in summer, parallel to the general coastline. However, there is considerable diversion in the Strait of Juan de Fuca where the southerly winds tend to blow seaward along the strait, while the northwesterly winds tend to blow inwards (Harris and Rattray, 1954).

In Juan de Fuca Strait the winds are limited by the geography, as in most of the coast inlets. The seaward, easterly winds are generally associated with southeast winds along the coast, and increase in strength to seaward. Reed (1931) suggested that these coastal winds had a venturi effect, accelerating the normally light easterly winds in the outer reaches of the strait. Out of 75 occurrences of winds greater than 50 mph at Tatoosh, the average was 60 mph. The average of the corresponding winds at Port Angeles was 16 mph.

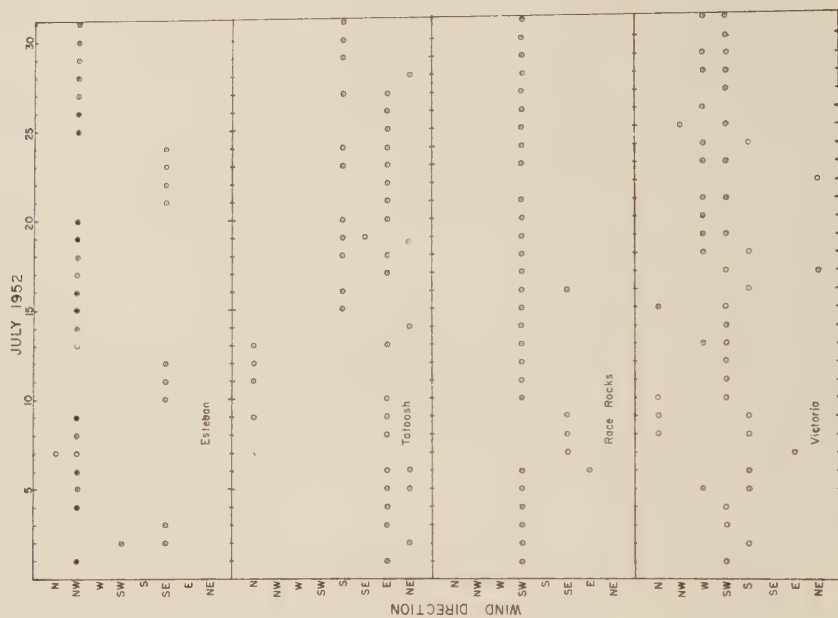


FIG. 7. Semi-daily observations of wind directions along the ocean coast and in the Juan de Fuca region.

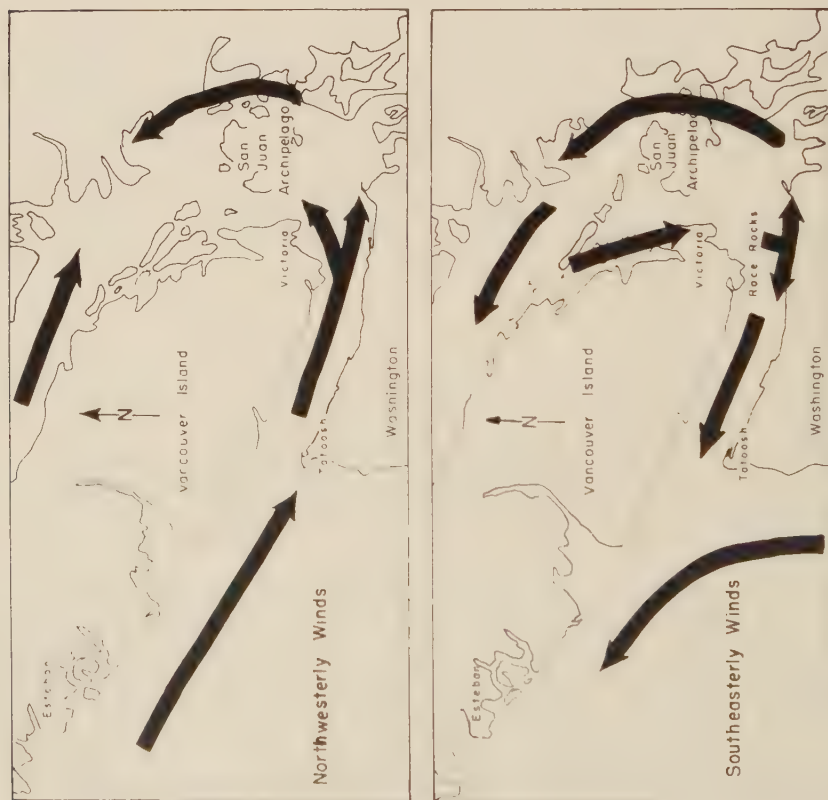


FIG. 6. Principal winds along the ocean coast and in the Juan de Fuca region.

The westerly winds, blowing inward in the strait, are usually associated with northwest winds along the coast. They are diverted and channelled up the strait by the orographic effect of adjoining mountains. However, they also occur as strong afternoon winds during summer, when the coastal winds are light. Generally these winds are strongest off Victoria and in the Inner Strait.

It may be deduced from a study of Fig. 7 and similar data that the winds at Tatoosh, at the entrance to Juan de Fuca Strait, are affected by the wind systems in the strait and along the coast. They show no definite trends, and evidently exhibit characteristics of both. Observations made during oceanographic surveys indicate that a few miles seaward of the entrance, the coastal winds, as recorded at Esteban (Estevan) Point, are dominant. A few miles into the strait, the Juan de Fuca winds, as recorded at Victoria or at points along the strait, are dominant.

The observed winds at Victoria (Fig. 1) through the period 1922 to 1946 have been summarized by Boughner and Thomas (1948) as shown in Table I.

TABLE I. Analyses of wind data from Victoria, B.C., January 1922–December 1945.
(Boughner and Thomas, 1948).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Percentage frequency (by directions)												
North	30	31	19	14	10	6	4	5	14	24	31	28
Northeast	18	15	10	9	6	4	4	5	10	12	15	14
East	14	12	10	8	6	4	4	5	8	11	14	14
Southeast	11	10	8	6	4	2	2	2	4	8	10	14
South	7	7	9	10	13	15	16	17	15	12	8	9
Southwest	7	8	16	22	29	34	40	37	21	12	11	7
West	11	14	24	28	30	33	29	26	24	17	12	12
Northwest	2	2	3	2	1	1	*	1	1	2	2	1
Calm	*	1	1	1	1	1	1	2	3	2	1	1
Average wind speed in miles per hour (by directions)												
North	10.4	10.3	10.0	9.0	8.5	7.1	5.5	6.1	7.2	8.7	9.2	9.7
Northeast	12.8	10.5	8.2	8.6	7.5	6.3	6.1	6.1	7.3	7.3	8.8	12.3
East	8.2	7.8	7.8	7.1	6.2	5.5	4.7	5.2	5.3	5.8	7.3	8.6
Southeast	16.1	16.8	14.3	12.5	11.2	7.0	5.4	6.1	8.4	12.2	15.8	17.7
South	10.8	8.9	8.1	7.8	8.6	9.2	8.4	8.4	6.9	7.2	9.3	11.7
Southwest	20.5	18.4	17.8	16.0	15.7	14.7	15.1	13.5	11.5	11.2	17.8	21.5
West	16.2	14.4	14.2	13.9	13.7	14.5	12.6	12.0	11.2	12.0	14.8	16.8
Northwest	7.0	6.3	6.3	6.5	5.0	4.7	3.6	4.1	4.5	5.0	6.5	6.4
Average wind speed in miles per hour												
	12.4	11.6	11.6	11.7	12.0	12.3	11.9	10.6	8.7	8.9	10.7	12.8

*Indicates less than 0.5%.

The analysis of percentage frequency shows that there is no direction from which the winds predominate. Rather, the outward-blowing winds (N, NE, E, SE) occur more than 50% of the time during the winter (October through March). The inward-blowing winds (S, SW, W) predominate during the summer (April

through September). Furthermore, the inward-blowing winds (westerly), whenever they occur, are always stronger than the outward-blowing (easterly) winds.

The principal oceanographic effect of the winds in Juan de Fuca Strait is to accelerate or retard the surface seaward transport. It is probable that the occasionally observed intrusions of ocean water along the southern side of the strait are associated with periods of westerly winds.

FOG

Figure 8 shows that the frequency of fog reaches its maximum from July through October, and is a minimum in the winter and spring months. From observations taken in 1952, there seems to be a tendency for the fog to hold to

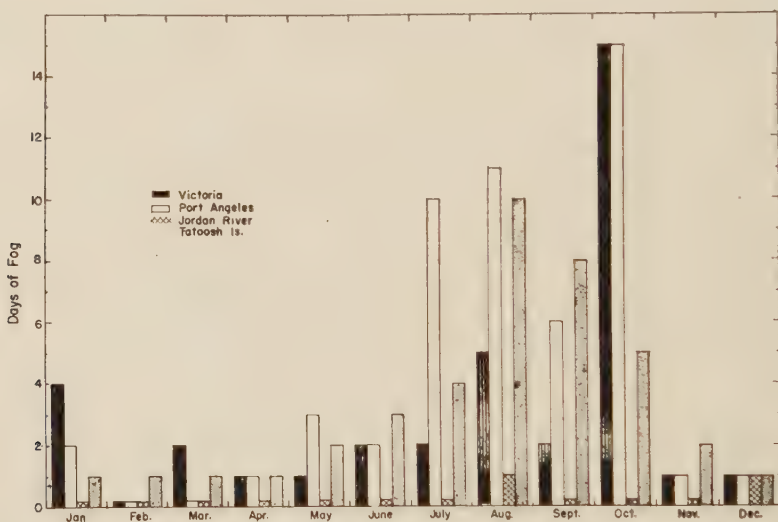


FIG. 8. Occurrence of fog in Juan de Fuca Strait at Victoria, Port Angeles, Jordan River and Tatoosh Island (1952).

the Washington side of Juan de Fuca Strait. This may be due to the cold air coming off the Olympics meeting the warm moist air coming in off the Pacific, or it may be due to the cool water intrusion from the sea along the Washington coast.

PROPERTIES AND STRUCTURE OF THE WATER INVESTIGATIONS

The properties of the water currents in Juan de Fuca Strait were observed at approximately bi-monthly intervals from October 1951 to October 1952, according to the plan shown in Fig. 2 (bottom diagram), and the schedule shown in Table II. This was a joint project carried out by the Pacific Oceanographic Group of the Fisheries Research Board of Canada, and the Pacific Naval

Laboratory of the Defence Research Board of Canada, in the oceanographic research vessel CNAV *Ehkoli*, operated by the Royal Canadian Navy. The whole undertaking was directed and published by the Joint Committee on Oceanography (1955). There was a series of observations (Fig. 2) across the strait and

TABLE II. Schedule of observations.

<i>Cruise number*</i>	<i>Period</i>
I	Oct. 2-13, 1951
II	Nov. 5-17, 1951
III	Feb. 28-Mar. 8, 1952
V	Apr. 16-25, 1952
VII	Jun. 3-13, 1952
IX	Jul. 10-17, 1952
X	Aug. 13-20, 1952
XI	Sep. 23-Oct. 2, 1952

*Cruise numbers are those given in the Data Record (Joint Committee on Oceanography, 1955).

across the mouths of the principal passages leading to the Strait of Georgia and Puget Sound. The stations in each section were observed in sequence while the tide was rising (or falling) and again during the opposite tidal phase on the same or following day. The bi-monthly repetition of the surveys provided periodic observations of the annual cycle of properties, while the semi-diurnal repetition provided an assessment of tidal variation.

At each station a cast was made with Mark III Fjarlie water sampling bottles (Fjarlie, 1953) at depths of 0, 2, 6, 10, 20, 40, 60, 100, 150, and 200 m, or as many of these as the depth of water allowed. The bottles carried Richter & Wiese reversing thermometers. The temperature readings were taken and corrected on board ship. Salinity samples were sealed (McCracken, 1956) and determined at the base laboratory (McCracken, 1955). Dissolved oxygen was determined by the modified Winkler method adapted for shipboard use by Tully (1949).

The oceanographic laboratories of the University of Washington (1954; 1956a,b,c) made regular monthly observations at a number of stations from 1934 through 1938, as well as a number of surveys in the area. These data have not been published, but were made available in manuscript form. Later data, 1952-56, have been published (University of Washington, 1954-1956) and have been used in this report.

The oceanography of the Strait of Georgia has been fully discussed by Waldichuk (1957) and Tully and Dodimead (1957). The properties of the water in the ocean approaches to Juan de Fuca Strait have been observed (Joint Committee on Oceanography, 1956) and some aspects of circulation have been discussed by Tully (1941).

DISSOLVED OXYGEN

Figure 9 shows the dissolved oxygen distribution and structure observed in June 1952. The lowest surface concentrations occurred in the Inner Strait in the vicinity of the passages through the San Juan Archipelago, and particularly those leading to Puget Sound. From the Inner Strait the surface oxygen concentration increased seaward. The cross and longitudinal sections show that the concentration decreased with depth, and the iso-oxy's sloped downwards to the north, i.e. to the right when looking seaward, in all parts of the system. The structure and range of concentration were markedly different in the Inner and Outer Straits. In the Inner Strait the concentration was moderate, from 5.5 to 7.5 mg/l with a uniform gradient from surface to bottom. This water (from surface to 150 m depth) was continuous with the water between 40 and 60 m depth in the Outer Strait. There was marked stratification from a high concentration in the upper zone, to the deep zone whose waters were less than 40% saturated with dissolved oxygen.

As indicated by the representative seasonal longitudinal sections in Fig. 10, the principal features of dissolved oxygen structure and distribution persist throughout the year, although the values and range of values vary somewhat. The monthly sequence of dissolved oxygen concentrations in the upper and deep zones of the Outer Strait have been assembled from all available data (1934–1952) in the bottom diagram of Fig. 10. In both the surface and the deep waters (100 m) there is a simple annual cycle with a maximum in later winter (end of February), and a minimum at the end of summer (September). The range of dissolved oxygen concentration from surface to 100 m depth appears to be greatest in July and least in February.

The cross-sections in Fig. 11 show that at any position in the strait the dissolved oxygen concentration was slightly less during the flood than during the ebb tidal phase. It is notable that the cross-channel slope of the iso-oxy's was most marked during the ebb. In the illustrated longitudinal sections (October) they indicate marked differences of structure in the vicinity of the sill. During the flood, the deep iso-oxy's from the Outer Strait advanced up the seaward slope of the sill, and waters having oxygen concentrations as low as 4.0 mg/l were continuous over the sill into the Inner Strait. During the ebb, the deep iso-oxy's in the Outer Strait were depressed, and waters having less than 4.8 mg/l were not continuous over the sill. The phenomenon occurred throughout the year, although the critical oxygen values varied with season as shown in Fig. 10.

SALINITY

Figure 12 shows the salinity distribution and structures observed in June 1952. The lowest salinities occurred in the passages through the San Juan Archipelago, and extended into the inner part of Juan de Fuca Strait. From there the salinity increased towards Admiralty Inlet and to seaward. The

cross and longitudinal sections show that the salinity increased with depth, and the isohalines sloped downward to the north, i.e. to the right when looking seaward in all parts of the system. The structure and range of salinity were markedly different in the Inner and Outer Strait. In the Inner Strait the salinity was everywhere less than 32‰. This water (from near surface to 150 m depth) was continuous with the water above 50 m depth in the Outer Strait. There it formed a distinct upper zone, separated by a halocline from a deep zone whose salinity exceeded 33.5‰.

As indicated by the representative seasonal longitudinal sections in Fig. 13, the principal features of salinity structure and distribution persist throughout the year, although the values, and the range of values, vary somewhat. The monthly sequence of salinities in the upper and deep zones of the Outer Strait have been assembled from all available data (1934–1952) in the last diagram of the Figure. In the surface waters there is a marked minimum in January and a broad minimum through June and July. Maxima occur in March and October. At 100 m depth there is a single annual cycle of salinity having a minimum near the end of February and a maximum in August. Evidently the range of salinity from the surface to 100 m depth is least in March (and November) and greatest in July (and January).

The cross-sections in Fig. 14 show that at any position the salinity is slightly greater during the flood than during the ebb tidal phase. The cross-channel slope of the isohalines is steepest during the ebb. In the illustrated longitudinal sections (October) they indicate marked differences of structure in the vicinity of the sill. During the flood the deep isohalines from the Outer Strait advance up the seaward slope of the sill, and waters of salinities 32 to 33‰ are continuous over the sill into the Inner Strait. During the ebb, the deep isohalines in the Outer Strait are depressed, and waters of salinity greater than 32‰ are not continuous over the sill. This phenomenon occurs throughout the year, although the critical salinity values vary with season as shown in Fig. 13.

ZONE STRUCTURE

Tully (1958) has shown that there are definite features of salinity structure associated with estuarine systems which distinguish the regimes of fresh and sea water: He noted that there usually was an *upper zone* in which the salinity was nearly constant to a limited depth, but increased seaward. Below this was a *halocline* which was most marked near the major fresh water sources, and became less distinct to seaward, as the salinity of the upper zone increased. Below this was a *lower zone* of saline (ocean) water which was nearly homogeneous from head to mouth of the seaway, and with depth.

He deduced that the halocline is due to internal mixing and in the absence of wind it would extend to the surface. Herlinveaux (1962) observed this structure in Saanich Inlet. In the presence of wind, the waters are mixed to



FIG. 9. Dissolved oxygen distributions and structures observed in Juan de Fuca Strait, June 1952.

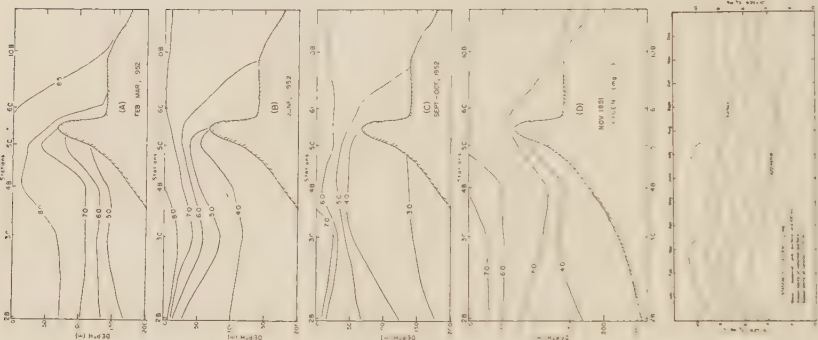


FIG. 10. Representative seasonal structures of dissolved oxygen observed in Juan de Fuca Strait, and the average monthly values at the surface and 100 m depth.

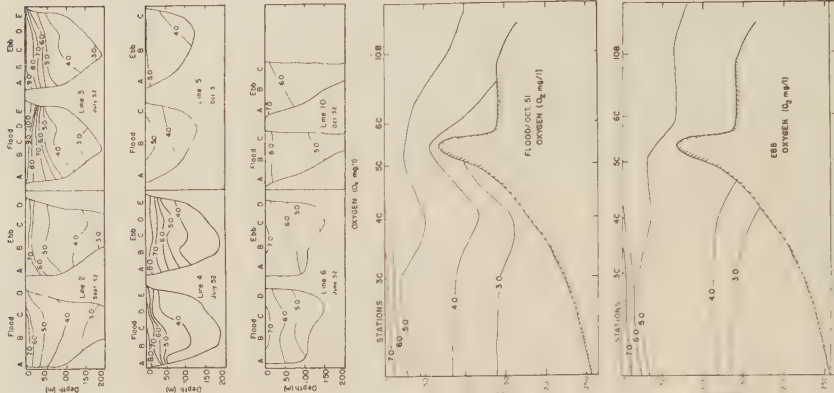


FIG. 11. Structures of dissolved oxygen observed in Juan de Fuca Strait during the flood and ebb phases of the tide.

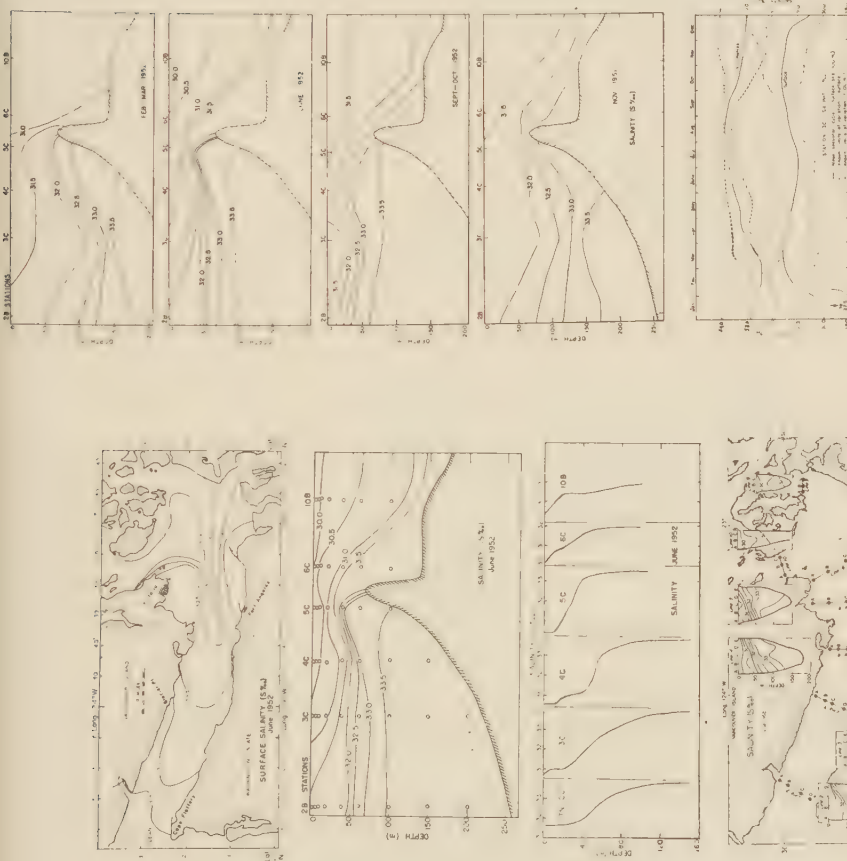


FIG. 13. Representative seasonal salinity structures observed in Juan de Fuca Strait and the average monthly values at the surface and 100 metres depth.

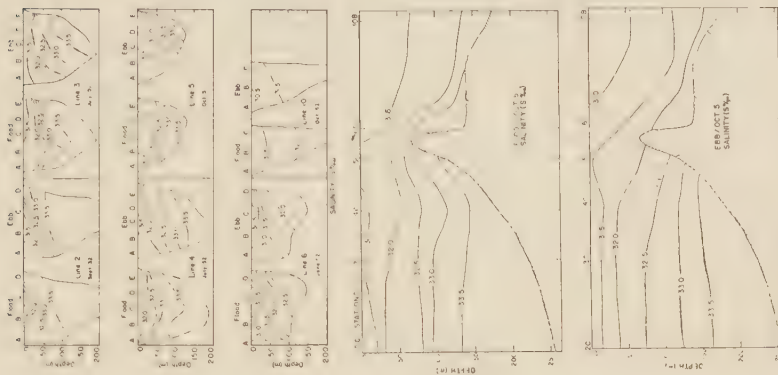


FIG. 14. Salinity structures observed in Juan de Fuca Strait during the flood and ebb phases of the tide.

FIG. 12. Salinity distribution and structures observed in Juan de Fuca Strait, June 1952.

homogeneity to the depth of wind influence, as Tully observed in Alberni Inlet, and Dodimead (1961) observed in the subarctic Pacific Ocean.

He also showed that when the observed salinities were plotted as functions of the logarithm of depth, the zones were defined by straight-line segments (Fig. 15) and their limits by the intersection of the segments. He designated the upper limit of the halocline as (D) and the lower limit as (L).

Tully (1952) studied this structure in Alberni Inlet where he found the zone structure simply defined as shown in the first diagram of Fig. 15. In the Strait of Georgia there was a step-structure of alternating homogeneous zones and haloclines. This resulted from the upper zone being successively over-run by successive fresh water outflows. The lower diagrams of the Figure show the zone structure in the outer basin of Juan de Fuca Strait. Here, there are two distinct segments in the halocline structure, which are characteristic of this region.

Figure 16 shows depths of the limits (D) and (L) in the several seasons. As in the corresponding salinity data (Fig. 12 to 14) there was a cross-channel slope of the surfaces, but no clear gradient to seaward.

Figure 17 shows the limits in mid-channel section. In the Outer Strait the zone structure can be identified, as shown in Fig. 15. However, in the Inner Strait the halocline extends effectively from surface to bottom. This structure is similar to that observed by Pritchard (1956) in the coastal plain estuaries of the Atlantic coast of the United States.

The depths and salinities at the limits (D) and (L) at Station 3C throughout the year are shown in Fig. 18, along with the runoff data. Here it is apparent that the characteristics of the upper limit (D) of the halocline are related to the runoff while those of the lower limit (L) are related to the cycle of salinity in the deep zone.

FRESH WATER BUDGET

It is evident that the system contains two fluids, fresh and sea water. It is of interest to consider the proportions of each.

The concentration (C) of fresh water in an interval of depth (Z_1-Z_0) at any position, is:

$$C = \frac{S^u(Z_1-Z_0) - \int_{Z_0}^{Z_1} S dz}{S^u(Z_1-Z_0)}$$

where S is the observed salinity and S^u is the salinity of undiluted ocean water. This has been called the base salinity by Waldichuk (1957) and the *Index Salinity* by Tully (1958).

Ignoring the zone structure, Waldichuk solved this relation through arbitrary depth intervals (0-10 m, 10-50 m, 50-100 m) along a section through the Strait of Georgia and Juan de Fuca Strait as shown in Fig. 19. From a study of the data he concluded that the index salinity 33.8‰ was representative of the ocean water being supplied to the system at the time (September 1952). Figure 18

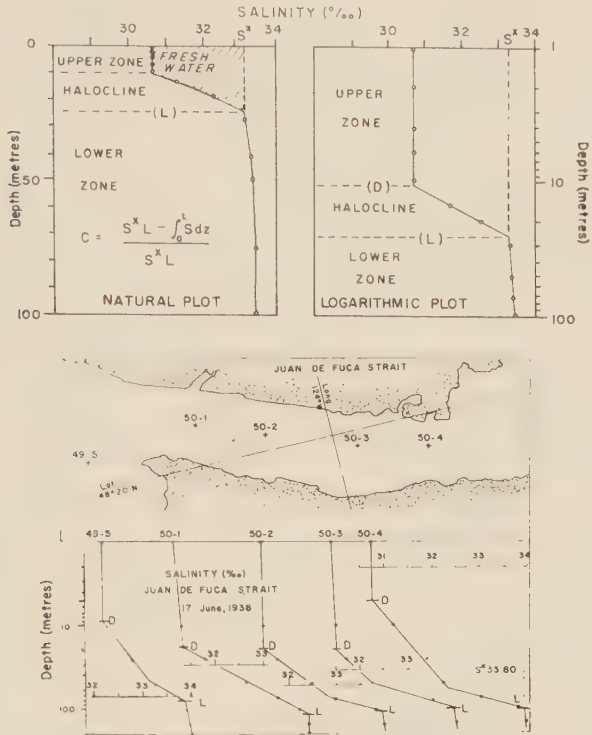


FIG. 15. Features of zone structure, and zones in Juan de Fuca Strait.

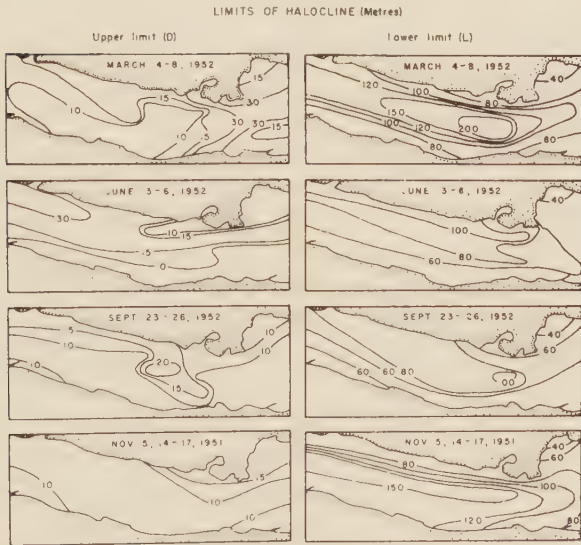


FIG. 16. Depth in metres of the upper (D) and lower (L) limits of the halocline in Juan de Fuca Strait.

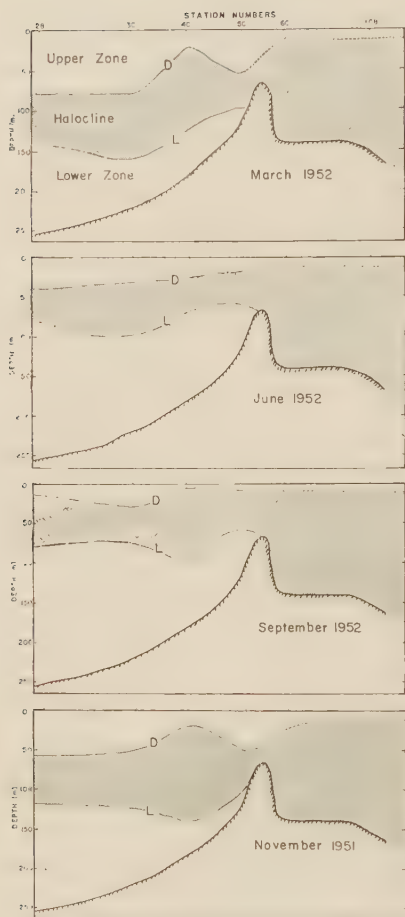


FIG. 17. Longitudinal sections of Juan de Fuca Strait showing the depth (metres) of the upper (D) and lower (L) limits of the halocline.

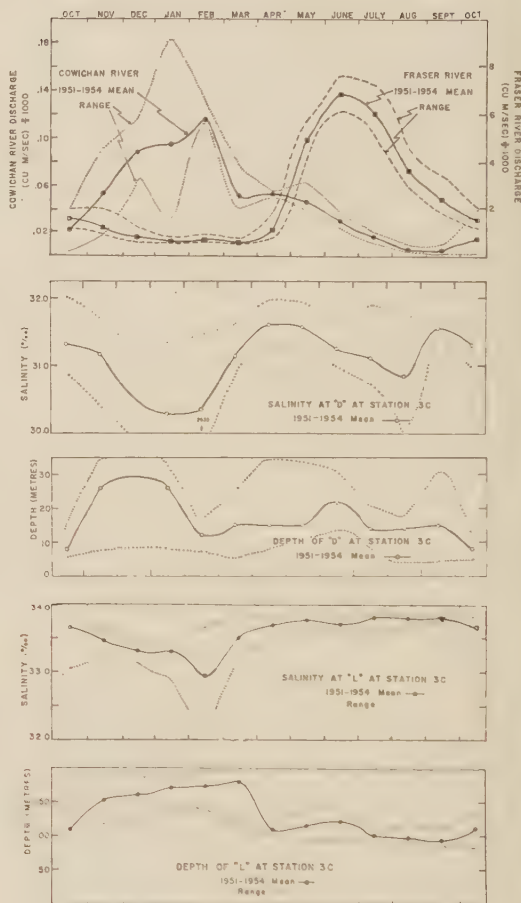


FIG. 18. Depth and salinity of the limits (D and L) of the halocline at station 3C, compared to the runoff and deep salinity.

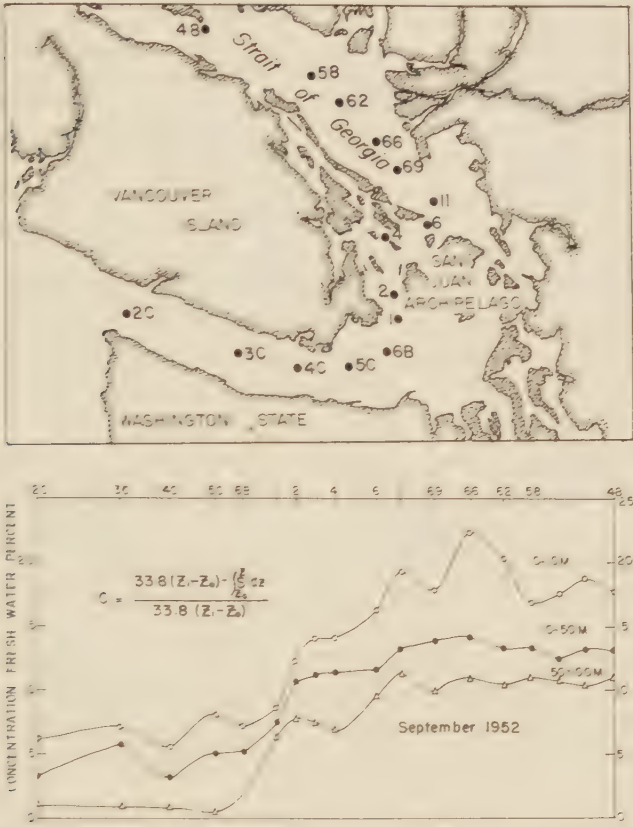


FIG. 19. Concentration (C%) of fresh water in a section through the Strait of Georgia and Juan de Fuca Strait, September 1952. (From Waldichuk, 1957.)

shows that this value coincides with the salinity at the lower limit of the halocline. He showed conclusively that the concentration (C) of fresh water decreased to seaward, and was a function of the depth interval ($Z_1 - Z_0$) considered.

Tully (1958) deduced that when fresh water enters an embayment it moves persistently seaward through the upper zone and halocline. En route it entrains sea water from the lower zone, where there is a persistent inward transport sufficient to supply the entrainment demand. It follows that *all* the local fresh water is contained above the limit (L). The lower zone contains only intruding sea water. The character of the water being entrained into the halocline is defined by the index salinity (S^*) at the limit (L) of the halocline. Then the concentration (C) of fresh water contained in the upper zone and halocline is:

$$C = \frac{S^*L - \int_0^L S dz}{S^*L}.$$

Re-arranging this equation, the total amount of fresh water at any position may be expressed as the depth (CL) of fresh water in a unit column segregated from sea water of index salinity (S^x):

$$CL = \frac{S^x L - \int_0^L S dz}{S^x}.$$

In practice, the depth of the lower limit (L) of the halocline and the corresponding index salinity (S^x) were determined in a logarithmic plot (Fig. 15). From these data a plot on a natural scale was made. Then the numerator of the equations was readily obtained by planimeter integration of the area between the salinity-depth graph, and the index salinity, as shown in the Figure.

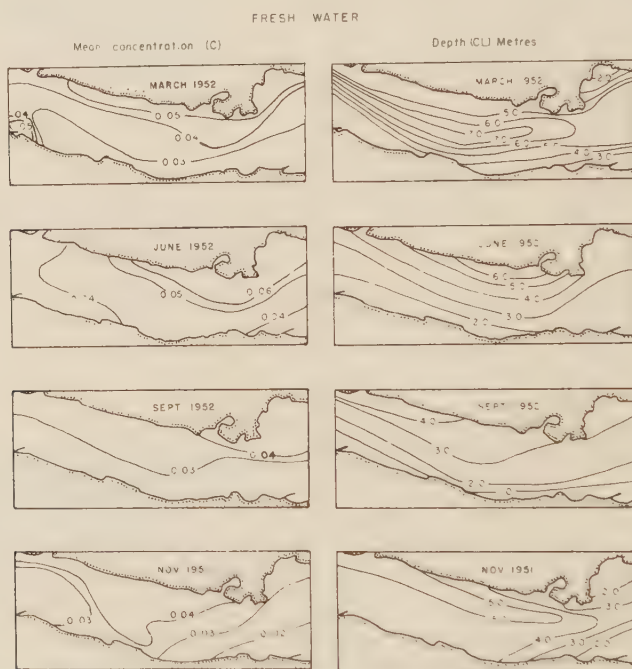


FIG. 20. The mean concentration (C) and the amount, or depth (CL metres) of fresh water contained in the upper zone and halocline in Juan de Fuca Strait.

Contours of concentration (C) and amount or depth (CL) of fresh water in the upper zone and halocline are shown in Fig. 20. Here S^x varies seasonally as shown in Fig. 18. These diagrams emphasize the cross-channel gradient of fresh water, and the lack of longitudinal gradients. Comparison with Fig. 19 shows that the concentrations of fresh water were similar to those computed by Waldichuk (1957) considering the difference in basis of computation.

TEMPERATURE

Figure 21 shows the temperature distribution and structures observed in June 1952. There was no marked horizontal gradient over the area, although the lowest surface temperatures occurred in the vicinity of the sill. The cross and longitudinal sections show that the temperature decreased with depth, and that the isotherms generally sloped downward to the north, in all parts of the system. The structure and range of the temperature were markedly different in the Inner and Outer Strait. In the Inner Strait the temperature was everywhere greater than 7.5°C and there was no distinct thermocline. This water, from surface to 150 m depth, was continuous with the water above 50 m depth in the Outer Strait. There it formed a distinct upper zone, separated by a thermocline from a deep zone, whose temperature was less than 7.0°C .

It is notable that the summer thermocline was coincident with the halocline; hence the zone structure, based on salinity, can be extended to temperature. This is quite different from conditions in the ocean, where Dodimead (1961) has shown that the thermocline structure occurs wholly within the upper zone.

As indicated by the representative seasonal longitudinal sections in Fig. 22 these features of temperature structure and distribution persist through spring, summer and autumn (June, September, November), although the range of values varies considerably. In winter (March) the structure is reversed, the coldest water being on the surface and the warmest in the depths. The monthly sequence of temperatures in the upper and deep zones of the Outer Strait has been assembled from all available data (1934–1952) in the bottom diagram of the Figure. In the surface waters there is a single annual cycle of temperature with a marked minimum in February and a broad maximum through June, July, and August. In the deep zone, as represented by the data from 100 m depth, there is a simple annual cycle, opposite in phase to that at the surface. A marked maximum occurs in January and a broad minimum occurs through the summer.

The temperature decreases with depth (negative gradient) from March to December, and the maximum range occurs in August. The temperatures increase with depth (positive gradient) from December to March and the range is greatest in February. The waters are generally isothermal in December and late March.

The cross-sections in Fig. 23 show that during the summer at every position, the water is slightly colder during the flood than during the ebb tidal phase. Further, the cross-channel slope of the isotherms is most marked during the ebb. In the illustrated longitudinal sections (October) the isotherms indicate marked differences of structure in the vicinity of the sill. During the flood, the deep isotherms from the Outer Strait advance up the seaward slope of the sill, and waters of temperatures 8 to 9°C are continuous over the sill into the Inner Strait. During the ebb, the deep isotherms in the Outer Strait are depressed and waters colder than 9°C are not continuous over the sill. This phenomenon occurs throughout the year, although the definitive temperatures vary with season as shown in Fig. 22.

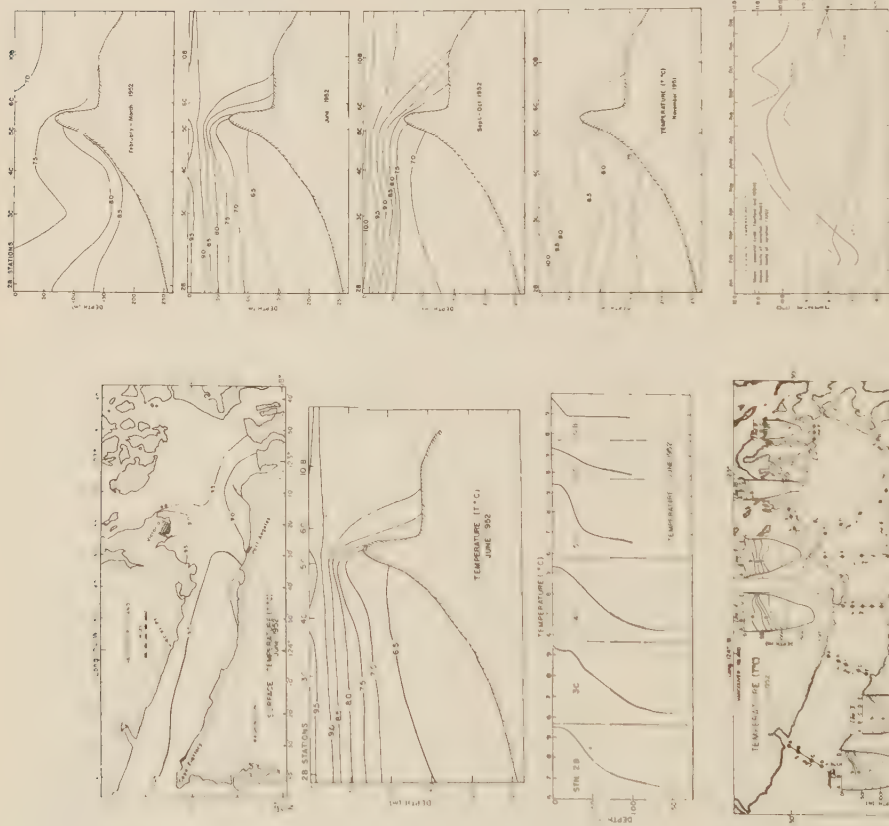


FIG. 21. Temperature distribution and structures observed in Juan de Fuca Strait,

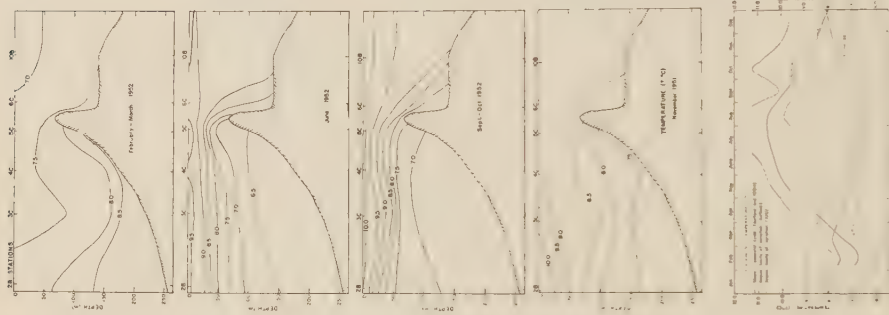


FIG. 22. Representative seasonal temperature structures observed in Juan de Fuca Strait, and the average monthly values observed

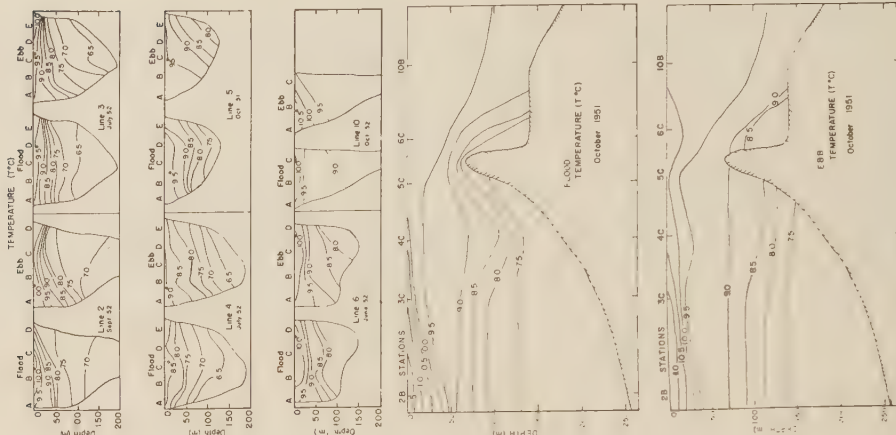


FIG. 23. Temperature structures observed in Juan de Fuca Strait during the flood and

HEAT BUDGET

Waldichuk (1957) studied the heat budget in the Strait of Georgia and Juan de Fuca Strait, on the basis of data observed in 1950. It is expedient to summarize some of the major features here for ready reference.

The net heat exchanges between the sea and atmosphere, computed from Waldichuk's data, are shown in Fig. 24. These include the heat gain from the sun, corrected for reflection and cloud cover; and the heat losses due to back radiation from the sea surface, evaporation, and conduction. These show that there is a heating situation through the warm months from the end of March through September. A cooling situation exists through the rest of the year. Further the heat exchange follows the same general cycle in the Strait of Georgia (Entrance Island) as in Juan de Fuca Strait (Victoria).

It may be argued that in a stagnant basin the water temperatures would be a simple function of the heat content, and would follow the integral of the heat-exchange curve. The maximum temperatures would occur in September and the minimum in March. This is not quite the case in Juan de Fuca Strait, as shown in the middle diagram of Fig. 24.

Waldichuk computed the discrepancy between the heat exchange and the heat contained in the water, and concluded that heat was being transported out of (and into) the system as indicated in the bottom diagram of Fig. 24.

While passing from the Strait of Georgia to Juan de Fuca Strait the surface water temperatures decrease in the San Juan Passages during the summer, as shown in Fig. 25. This decrease in surface temperature is due to the extensive tidal mixing in the passages. As the shallow (10-m) warm upper zone progresses seaward, it is mixed to near homogeneity with almost 100 m of cool lower-zone water. Hence there is a heat transport out of the Strait of Georgia. In winter (March) the relation is reversed because the surface waters of the Strait of Georgia become colder than the deep waters. At this time there is a heat transport into the region.

DENSITY²

Figure 26 shows examples of the density (σ_t) structures observed in June 1952. The lowest values occurred in the passages through the San Juan Archipelago, and extended into the Inner Strait. From there, the density increased toward the Washington State side of the strait and to seaward. The cross and longitudinal sections show that the density increased with depth, and the isopycnal surfaces sloped downward to the north, in all parts of the system. The structure and range of density were markedly different in the Inner and Outer Strait. In the Inner Strait, σ_t was everywhere less than 25.0. This water (from surface to 150 m depth) was continuous with the water above 50 m depth in the Outer Strait. There it formed a distinct upper zone separated by a pycnocline from a deep zone whose σ_t value exceeded 26.5.

²In this paper density is expressed as $\sigma_t = (\text{specific gravity}-1)1000$ (Sverdrup *et al.*, 1946).

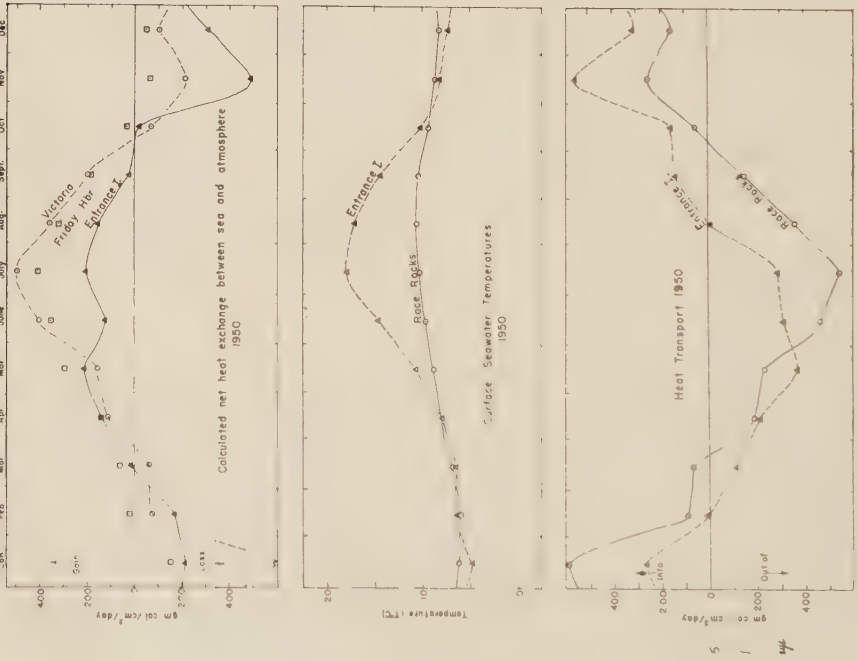


Fig. 24. Heat exchange between the sea and atmosphere, and resultant seawater temperature at locations in the Strait of Georgia and Juan de Fuca Strait, and heat transport into and out of the system (from Waldichuk, 1957).

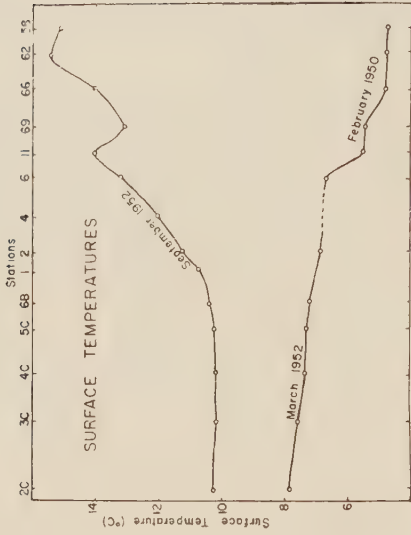


Fig. 25. Surface water temperatures through the Strait of Georgia and Juan de Fuca Strait in September and March 1952.



FIG. 28. Density (σ_t) structures in Juan de Fuca Strait observed during the flood and ebb phases of the tide.

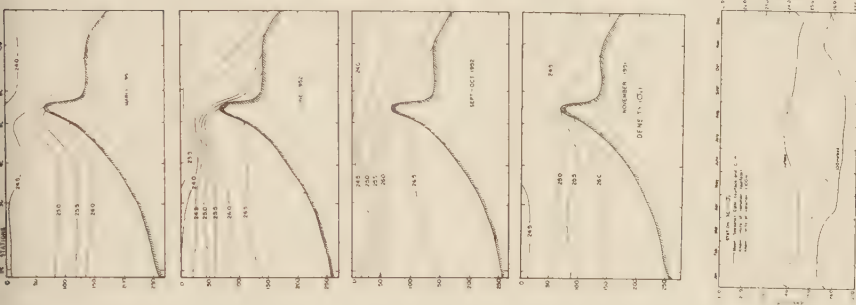


FIG. 27. Representative seasonal density (σ_t) structures observed in Juan de Fuca Strait, and the average monthly values at the surface and 100 metres depth.

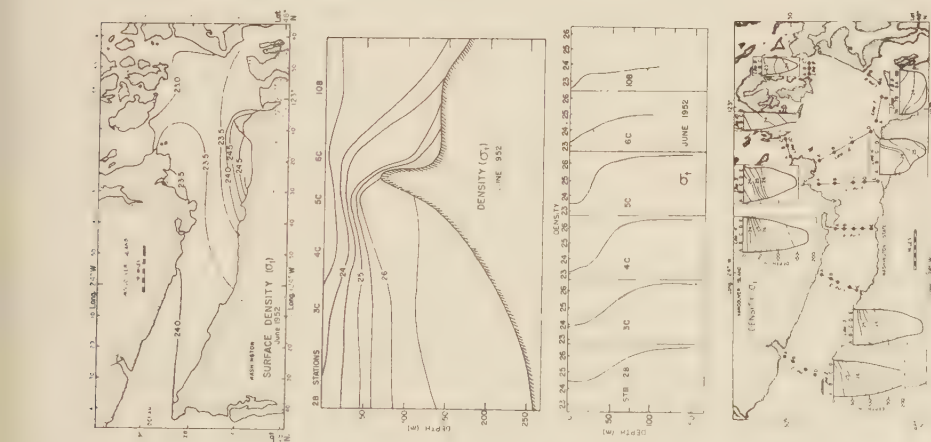


FIG. 26. Density (σ_t) structures observed in Juan de Fuca Strait, June 1952.

As indicated by the representative seasonal longitudinal sections in Fig. 27 the principal features of density structure and distribution persist throughout the year, although the values and range vary somewhat. The monthly sequence of density in the upper and deep zones of the Outer Strait have been assembled from all available data (1934–1952) in the last diagram of the Figure. In the surface waters there is a marked minimum in January and a broad minimum through June to July. Maxima occur in early and late winter. At 100 m depth there is a single annual cycle of density having a broad minimum in winter and a maximum in summer. Evidently the range of density from surface to 100 m depth is least in February and November and greatest in July and January.

The cross-sections in Fig. 28 show that at any position the density is slightly greater during the flood than during the ebb tidal phase. The cross-channel slope of the isopycnal surfaces is most marked during the ebb. In the illustrated longitudinal sections (October) they indicate marked differences of structure in the vicinity of the sill. During the flood the deep isopycnals from the Outer Strait advance up the seaward slope of the sill, and waters of σ_t 25.0 to 26.0 are continuous over the sill into the Inner Strait. During the ebb the deep isopycnals in the Outer Strait are depressed, and waters of σ_t greater than 25.0 are not continuous over the sill. This phenomenon occurs throughout the year, although the definitive density values vary with season as shown in Fig. 27.

RELATION OF TEMPERATURE AND SALINITY TO DENSITY

Throughout this seaway system the influence of temperature on the density structure is always secondary to the effect of salinity. This is illustrated in the scatter diagrams of Fig. 29 which show the relations of the observed temperature and salinity to σ_t (density) in the outer and inner parts of Juan de Fuca Strait, and in the Strait of Georgia. It is evident that there is a very close relation between salinity and density, but no clear relation with temperature.

In both the Strait of Georgia and Juan de Fuca Strait there are vertical temperature gradients in summer, coincident with the salinity gradients. The only effect is to reinforce the density structure which is predetermined by the salinity gradients. In winter, the temperature gradients vanish, and the density structure is determined solely by the salinity.

WATER MASSES

Following the procedure of Helland-Hansen (1916) the relations of temperature to salinity were plotted using the comprehensive data from Line 3 in July 1952. Each station (A, B, C, D, E) was observed 10 times during the week July 2 through 7. The top row of diagrams in Fig. 30 shows that, except for the surface observations, the relations were linear, and coincident within 0.1 C°. Since each observation was made at a different time of day, the surface values varied in accord with the diurnal heating and cooling cycle (Tully and Dodimead, 1957). At greater depths the temperature may be regarded as a conservative

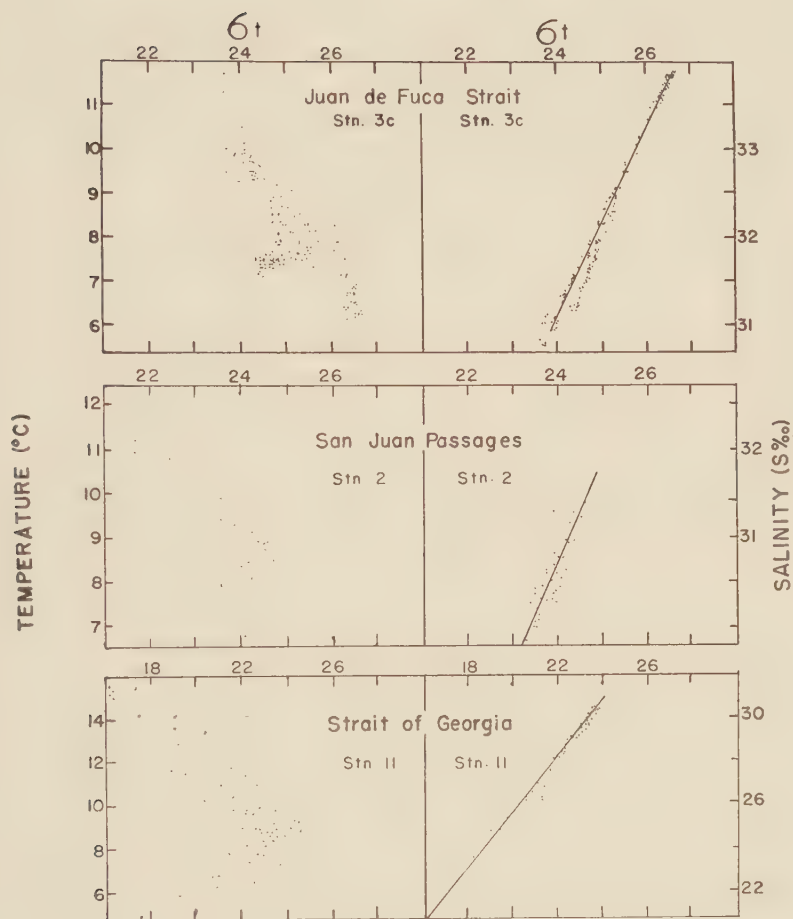


FIG. 29. Relation of temperature and salinity to density in Juan de Fuca Strait, the San Juan Passages, and the Strait of Georgia.

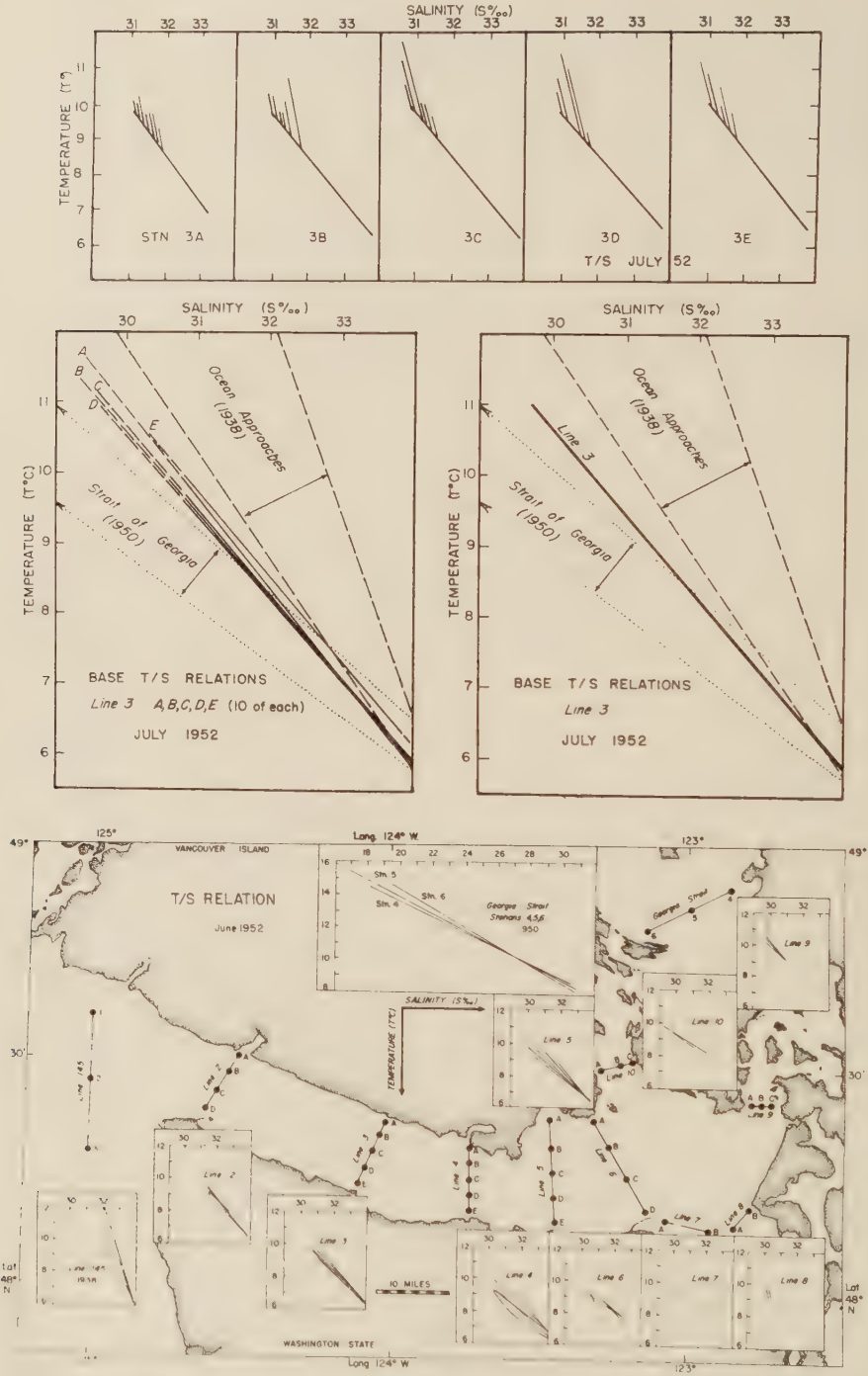


FIG. 30. Temperature-salinity relations at Line 3 in Juan de Fuca Strait, with reference to surrounding areas.

property, similar to salinity. Evidently the linear parts of these curves may be regarded as *base relations* at each station at this time.

In the middle diagrams of Fig. 30 these representative curves are brought together, ignoring the surface deviations. They form a tight bundle which can be represented by a single line (right-hand diagram) within $0.2\text{ }^{\circ}\text{C}$. This may be regarded as the *base relation for Line 3* at this time.

The bottom diagram of Fig. 30 shows the base relations for each station observed during the June survey. In general the relations are similar to those shown for Line 3 in July.

In Fig. 31 the base relations for each line of stations are assembled for comparison. It is evident that they form a fan of decreasing slope from the ocean

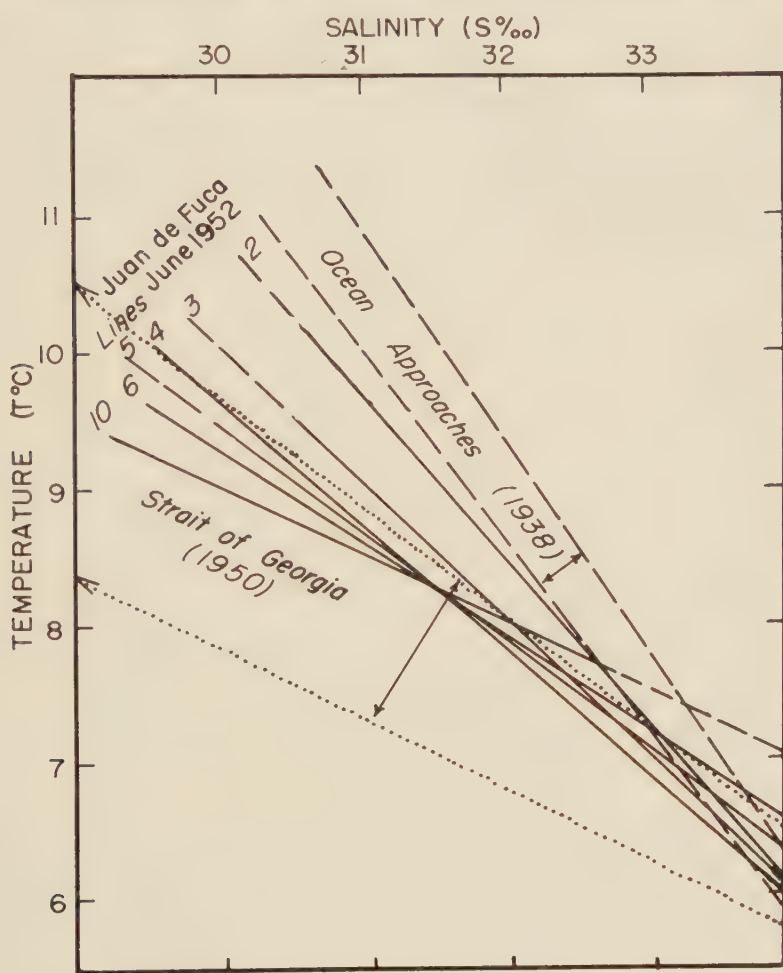


FIG. 31. Base temperature-salinity relations in Juan de Fuca Strait (June 1952) and limits of the relations in the Strait of Georgia (June 1950) and the ocean approaches (June 1938).

approaches at Line 2, to the passages through the San Juan Archipelago at Line 10. The regular sequence is marred only by the position of Lines 7 and 8 in the approaches to Admiralty Inlet, which are not shown.

For purposes of comparison, the envelopes of the data observed in the southern part of the Strait of Georgia in June 1950 (Joint Committee on Oceanography, 1954) and in the ocean approaches to Juan de Fuca Strait in June 1938 (Joint Committee on Oceanography, 1956) were added. There were no corresponding data from these neighbouring regions in June 1952. However, these are consistent with other data from these areas over a period of several years and may be considered representative of the character of these waters in June. The limiting character of the deep water at salinity 33.8‰ is identical throughout the system. At any temperature level above 7.3°C the Strait of Georgia waters are notably less saline than the coastal ocean water. It is at once evident that in Juan de Fuca Strait, the connecting seaway between these two distinct regions, these two water masses are progressively mixed.

In February and March when the upper waters are coldest the distinction between the water masses from the Strait of Georgia and the ocean approaches depends primarily on the salinity characteristics. These are illustrated in Fig. 32. The T-S diagrams at each station in Line 3 forms a tight bundle as before,

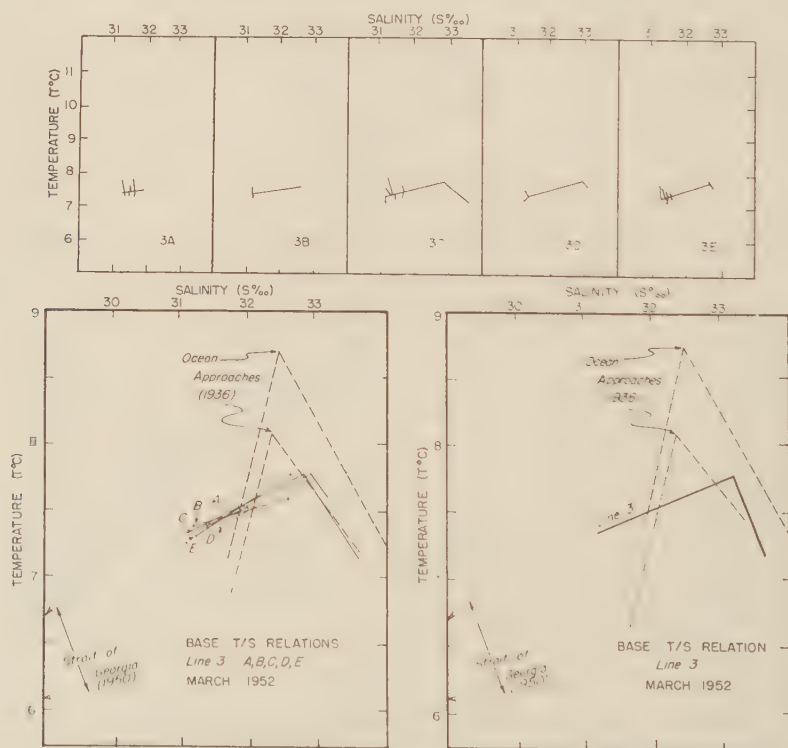


FIG. 32. Base temperature-salinity relations at Line 3 in Juan de Fuca Strait (March 1952).

but the slope is near zero or slightly positive, indicating that the temperature distinction had vanished at this time. Similar data are collected in Fig. 33 to show that the characteristics of the water masses are graded along Juan de Fuca Strait from the Strait of Georgia to the ocean approaches. It is evident that the gradation exists in winter as well as summer. Evidence from the other surveys shows that this gradation exists throughout the year.

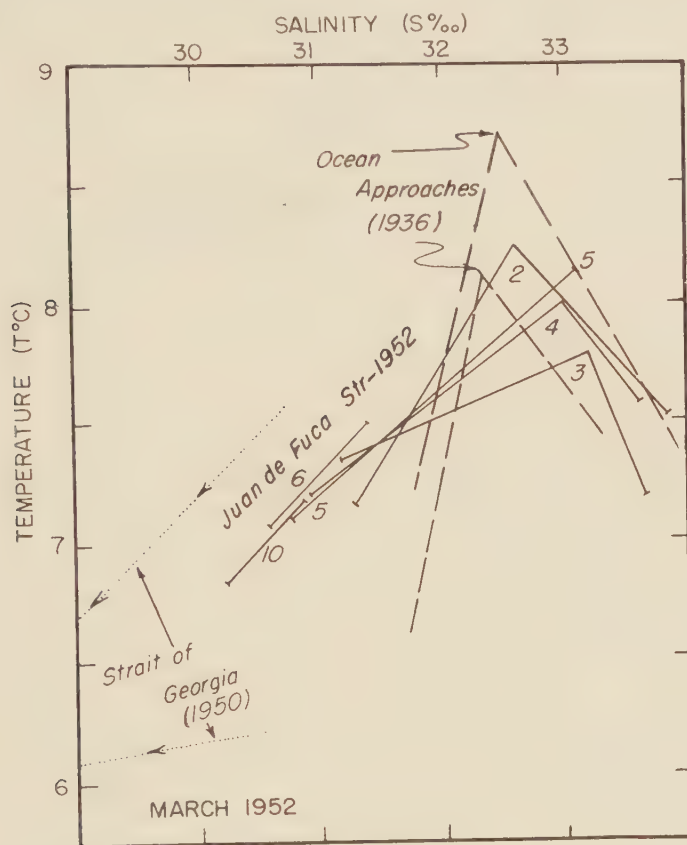


FIG. 33. Temperature-salinity relations in Juan de Fuca Strait (March 1952), the Strait of Georgia (March 1950) and the ocean approaches (March 1936).

The upper diagram of Fig. 34 shows the representative monthly base relations in mid-Outer Strait (Station 3C) compiled from all available data (1934-1952). These form an annual cyclic pattern which is emphasized in the lower diagram, where only the near-surface (2-m) and deep (100-m) data are shown. The configuration of these curves results from the annual cycles of salinity and temperature in the surface and deep waters which have been discussed already.

Recalling the gradient of T-S relations along the strait as shown in Fig. 31, it would be anticipated that the slope of the relation at any fixed position in the

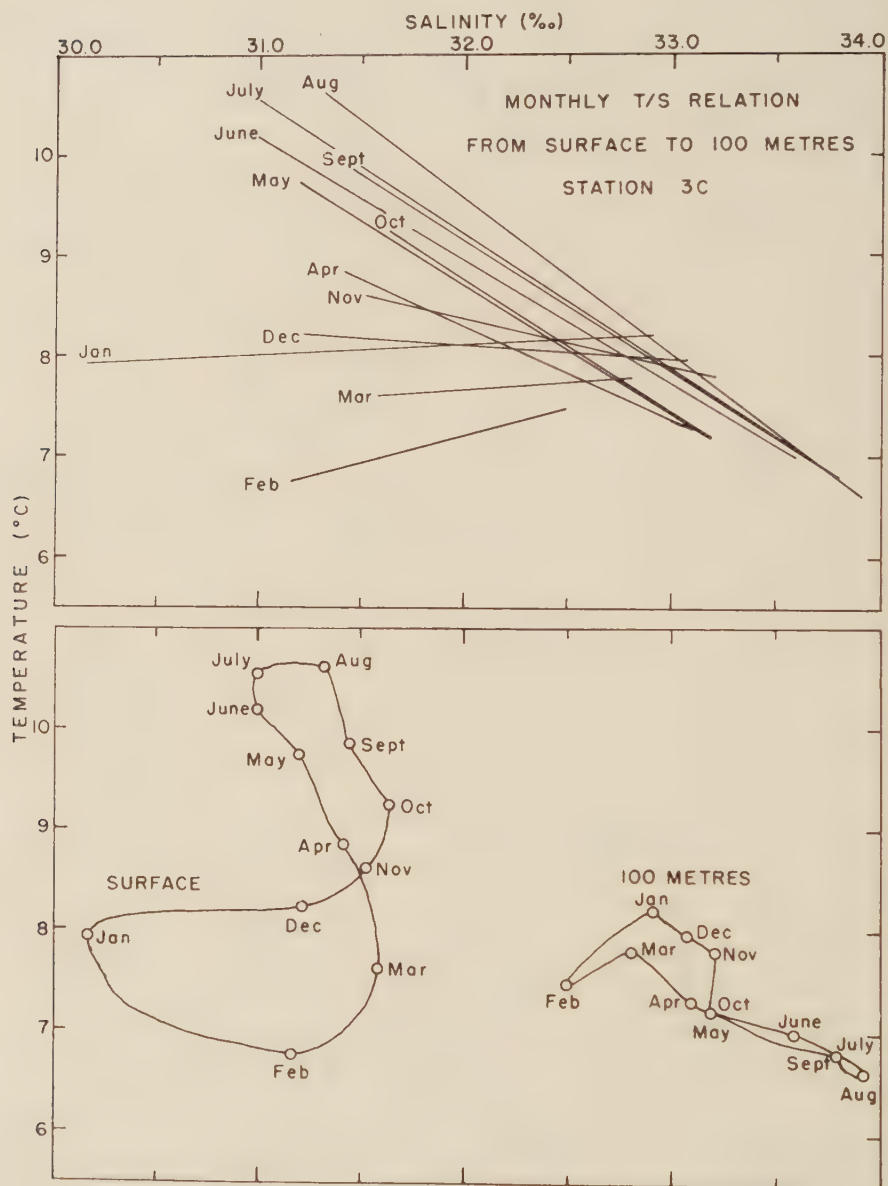


FIG. 34. Representative monthly temperature-salinity relations at Station 3C in Juan de Fuca Strait, and the annual cycle of relations at the surface and 100 metres depth.

strait would alter towards the character of the Strait of Georgia water during the ebb flow, and towards the character of ocean coastal water during the flood flow. The phenomenon is illustrated, with data from Station 3C, in the lower diagram of Fig. 35. In the vicinity of the sill (Line 5) the effect is most marked (as shown in the upper diagram) because the deep coastal water intrudes during the flood, and retreats during the ebb flow. This phenomenon is confirmed in all the data, and accounts for the variation (± 0.1 C°) between the several curves forming the base relation at each station (Fig. 30).

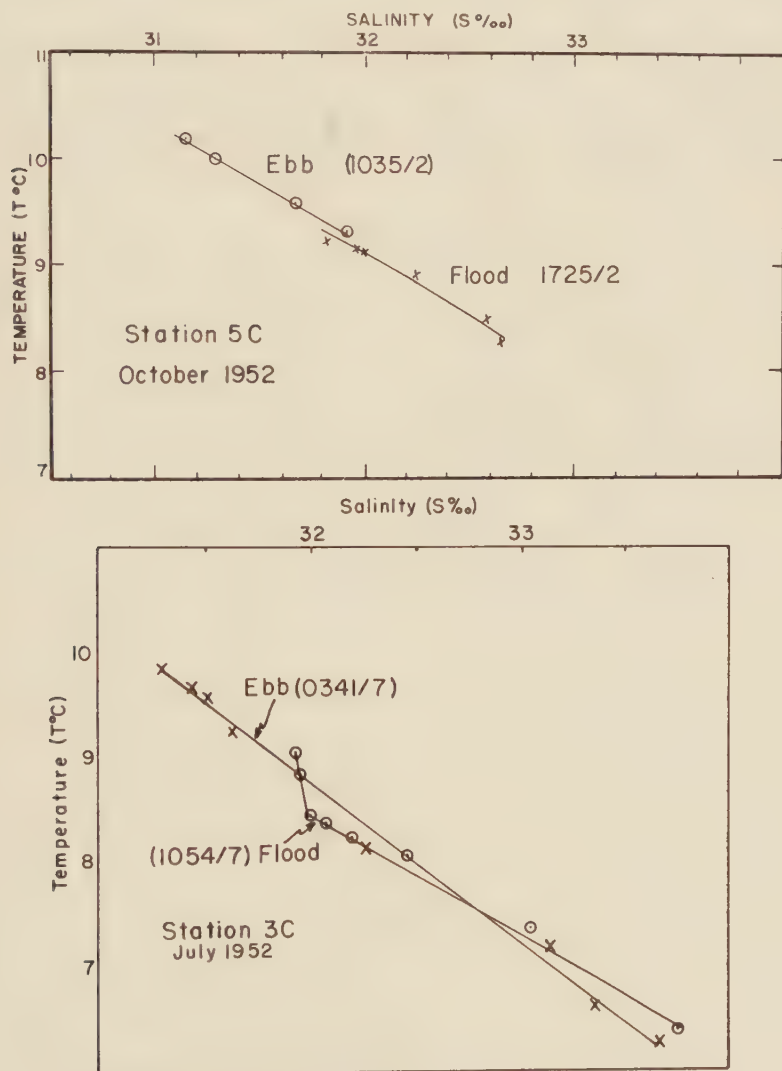


FIG. 35. Temperature-salinity relations at Stations 5C and 3C in Juan de Fuca Strait during the flood and ebb phases of the tide.

At locations of corresponding depth, the curves are longest where stratification is greatest (Fig. 30) in the Outer Strait (Lines 2, 3, and 4) and in Haro Strait (Line 10). The curves are short in the locations of greatest mixing where the waters are most nearly homogeneous, as in the vicinity of the sill (Lines 5 and 6). The curve is short in Rosario Strait (Line 9) because the location is shallow and admits only upper water of the same character as the upper water of Haro Strait (Line 10).

Consideration of these data indicates that the temperatures of the upper waters are seasonal features while the salinity is definitive of locality throughout the year.

If the temperature and salinity are observed at two depths, one near the surface and the other near the bottom, the relation and length of the curve are defined. Intermediate values of salinity may then be interpolated from a bathythermogram with considerable accuracy ($\pm 0.1\%$) through periods of several days. This facilitates routine observations, particularly time series, in the area.

OBSERVED CURRENTS AND STRUCTURES

The tides and tidal currents are major oceanographic features of Juan de Fuca Strait. However, the principal interest in this paper is the relation of the tidal phenomena to the properties and structure of the waters. In this deep seaway the tidal rise is a small fraction of the total depth, and in itself has little effect on the properties or structure of the waters, except in shallow near-shore areas. However, the ebb and flood tidal streams and the residual currents are major considerations.

The tides and tidal streams in Juan de Fuca Strait are of the mixed type with a marked semi-diurnal inequality. Throughout the seaway the tide occurs mainly as a standing oscillation, being high along the ocean coast when it is low in the Strait of Georgia and vice versa. In these circumstances the tidal streams are strongest at half tide, and flow towards the region where the tide is rising. The criteria and features of such situations have been discussed by Doodson and Warburg (1941) and are immediately apparent from an examination of the Tide and Current Tables (Canadian Hydrographic Service, Annual).

Herlinveaux (1957) studied these data. The average tidal speeds pass through semi-monthly cycles associated with the moon's phases. He observed that the near-surface temperatures and salinities followed similar cycles. The salinities increased during periods of maximum flow. In summer, the temperature decreased, and in winter it increased during these periods. He concluded that these effects were caused by mixing of the near-surface and deep water, and that the mixing forces were dependent on the speeds of tidal flow.

Herlinveaux (1954) also observed the velocity of flow (tidal streams plus residual currents) at intervals from the surface to near bottom, at three positions (A, B, and C) across Juan de Fuca Strait in the vicinity of Line 3 (Fig. 2) during March, July and October of 1952. From these data he deduced the distribution

of the velocity of flow through the cross-section at hourly intervals through a representative tidal day (Fig. 36). It is evident that the tidal streams flood and ebb at all depths.

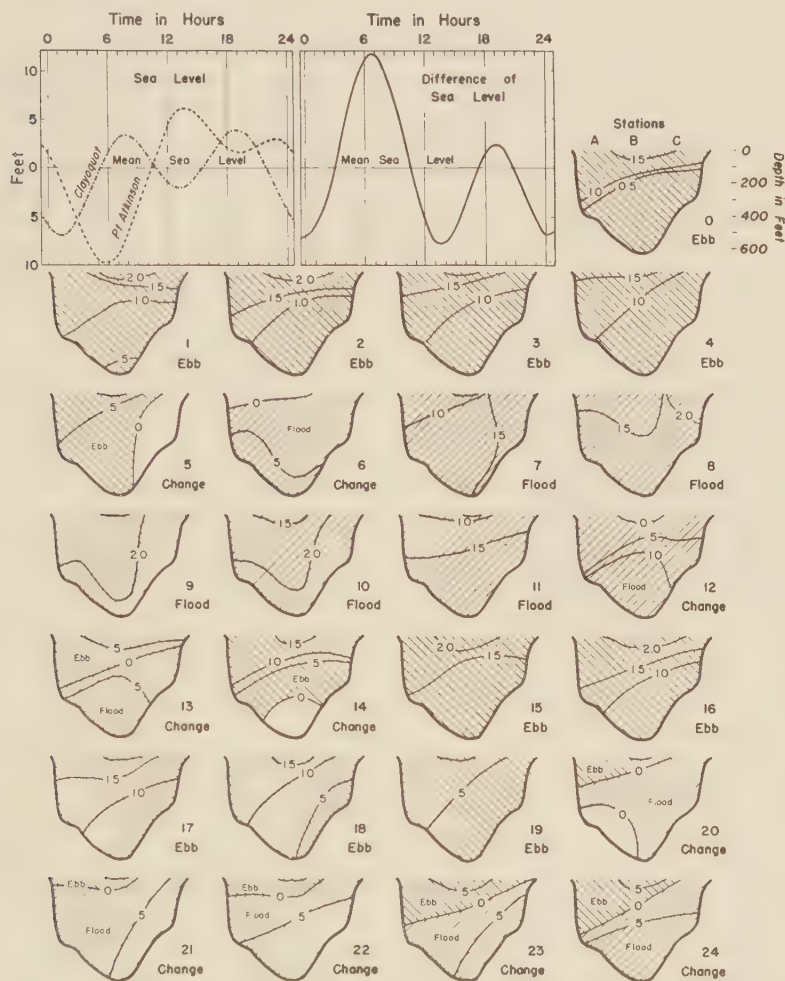


FIG. 36. Flow velocities through a cross-section (Line 3) of Juan de Fuca Strait, at hourly intervals (after Herlinveaux, 1954).

The mean flow velocities in the flood and ebb directions, from surface to near bottom in mid-strait (Station B) are shown in the upper diagram of Fig. 37, along with the net or residual current.

At this location, the residual current sets seaward in the upper 70 m of depth. Below this, the current is inward. This current structure has been discussed in some detail by Tully (1958). He showed that when the fresh water from land drainage enters the sea it moves seaward at the surface, entraining sea

water en route, to form a brackish upper zone. The dimensions of this zone are determined by the rate of mixing of fresh and sea water by the tidal streams and wind. In the upper zone and halocline, the residual current must set persistently seaward, else fresh water would accumulate in the system. In the lower zone ocean water intrudes at a rate sufficient to supply the demand for entrainment into the upper zone. Hence the residual current in the lower zone must be inward, and there must be a depth of no-net-motion between them. These conclusions are confirmed in Herlinveaux's data.

The lower diagram in Fig. 37 shows that the depth of no-net-motion was deepest (110 m) on the northern side of the strait (Station A) and shallowest (40 m) on the southern side, owing to Coriolis force. Hence the seaward transport of light water is greatest on the northern side, and the inward transport of dense water is greatest on the southern side.

It is desirable to consider the features of the transport (residual current) in relation to the tidal flow. However, as this cross-section is the only place where the flow at all depths has been determined, it is necessary to deduce the flow elsewhere in the seaway from the descriptions of surface flow given in the British Columbia Coast Pilot (Canadian Hydrographic Service, 1959), and the knowledge of the properties and structure of the water.

During the flood flow the excursion³ in all parts of the system is inwards as shown in Fig. 38. Ocean water intrudes the outer part of Juan de Fuca Strait. Being more dense (saline) it under-runs the upper zone, and contributes to the lower zone. From consideration of the properties, it is evident that the deep Juan de Fuca waters, below 100 m depth, are continuous with the ocean waters at 150 to 200 m depth. It is probable that the deep inflow migrates up the canyon through the approaches (Fig. 2).

In the Outer Strait this ocean water intrudes along the bottom, below the level of no-net-motion, carrying the upper zone water backward against its seaward tendency. Consequently the largest currents during the flood are in the lower zone as shown in Fig. 36 and 37.

The channel of the Outer Strait is slightly curved such that both the Coriolis and centrifugal forces act together to influence the flood flow toward the southern side, where it is stronger and flows for a longer period than on the opposite side. Thus the flood flow slackens first on the northern side, as observed by Herlinveaux (1954).

From the Outer Strait the waters move over the sill into the Inner Strait. The flow must be accelerated because of the vertical constriction of the channel. Although it is not visible at the surface, there must be considerable turbulence in the wake of the sill, extending into the Inner Strait during the flood flow. The seawater structures (Fig. 11, 14, 23 and 28) indicate that the ocean water

³The excursion of the tide is the distance travelled by a parcel of water during a period of inward (flood) flow, or outward (ebb) flow.

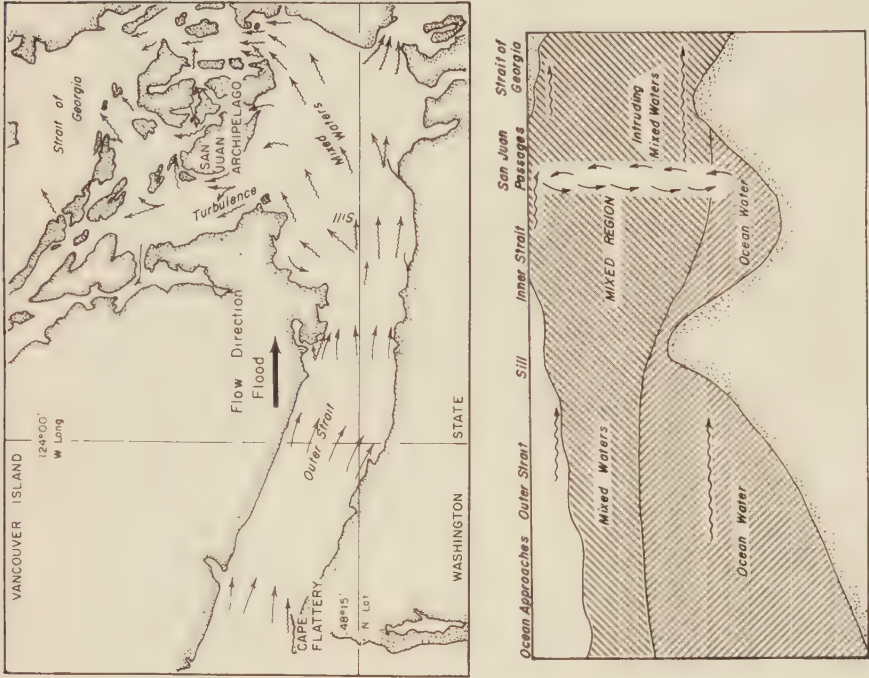


FIG. 38. Features of the flood excursions of the flow in Juan de Fuca Strait and approaches.

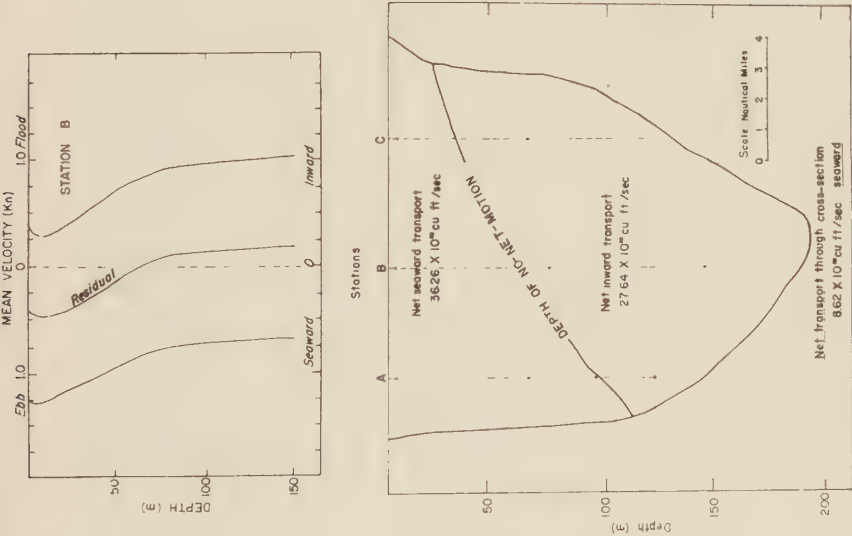


FIG. 37. Features of the mean tidal motion at Line 3 in the Outer Strait of Juan de Fuca Strait (after Herlinveaux, 1954).

rides up the seaward slope of the ridge and cascades into the Inner Strait. The data show that the greater part of this ocean water intrudes over the southern end of the sill where it is deepest (Fig. 2), a lesser part crosses in mid-channel, and little or none crosses the shallow northern end of the sill near Victoria. It is probable that this deep ocean water is carried forward over this obstruction partly by its momentum, and partly by the venturi effect of the stream over the sill.

In this process the halocline that was evident in the Outer Strait (Fig. 13, 14 and 17) is largely destroyed as the upper and deep-zone waters are mixed in the submerged wake stream in the Inner Strait. A small degree of stratification remains, and the salt content of the Inner Strait waters is replenished. It is probable that there is a thin zone of ocean water lying in the bottom of the deep channel through the Inner Strait (Fig. 2) but no observations were made to detect this.

The flood flow is mainly confined to the southern half of the strait and an eddy is formed in the approaches to Victoria. This is a region of strong streams and tide rips, though less violent during the flood than during the ebb.

From the Inner Strait the waters move into the San Juan Passages. The flow is strong (3 to 5 knots at strength) and there is visible turbulence (eddies and boils) particularly near the shores and in the narrower channels. The slight stratification observed in the Inner Strait vanishes and the waters attain virtual homogeneity by the time they reach the northern end of the passages (Tully and Dodimead, 1957).

From the San Juan Passages the flow enters the quiet stratified waters of the Strait of Georgia as jets. The momentum of the flow is quickly dissipated in the spectacular turbulence (Waldichuk, 1957) and internal waves (Shand, 1953) associated with the wake stream (Fig. 39). The mixed waters under-run the upper zone of the Strait of Georgia, and become the lower zone (Waldichuk, 1957).

During the ebb flow (Fig. 40) the excursion in all parts of the system is seaward (5 to 10 miles)⁴. The waters from the Strait of Georgia move into the San Juan Passages. Here the velocities reach 3 to 5 knots on the large tides. Turbulence is apparent in "boils" and "eddies" throughout the area. The upper and lower zone waters are mixed to near homogeneity.

The waters from the San Juan Channels issue as jets, accompanied by violent tide rips in the Inner Strait. As the rate increases to its maximum, the ebb stream must expand across the strait. This conclusion is supported by the observations of a convergence region, marking the shear zone between the opposing streams. The convergence moves from near Victoria towards the southern shore as the seaward flow develops. The flow from Haro Strait tends to cross the Inner Strait and converge with the stream from Rosario Strait, which

⁴Distance is measured in nautical miles (1 minute of latitude = 6080 feet = 1.853 km) in keeping with the use of Mercator charts. Velocities are measured in knots (50.2 cm/sec).

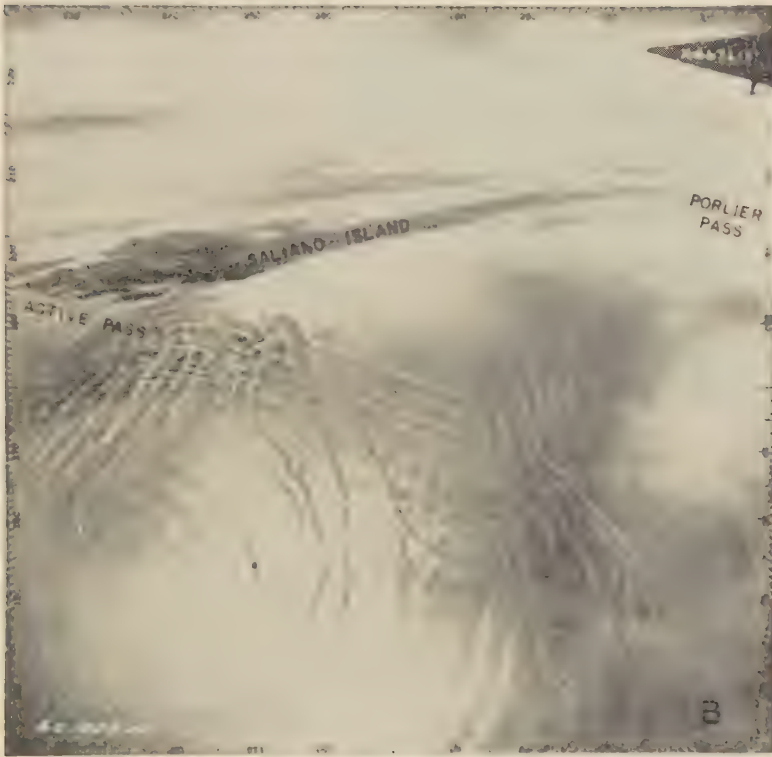
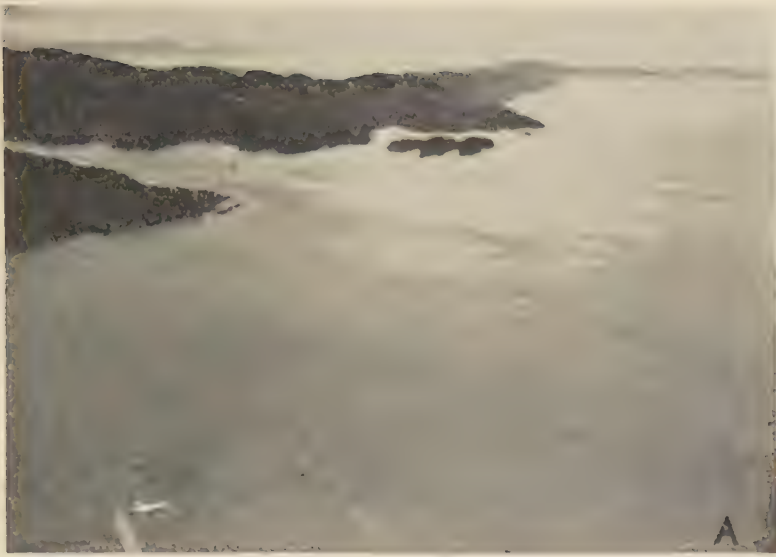


FIG. 39. (A) Aerial photograph of Active Pass, B.C., showing the jet stream of the flooding tidal current into the Strait of Georgia. (B) Aerial photograph of the Strait of Georgia showing the banded pattern attributed to internal waves generated by the flood jet flow from Active and Boundary Passes, (after Shand, 1953).

(Courtesy Pacific Naval Laboratory and Royal Canadian Navy.)

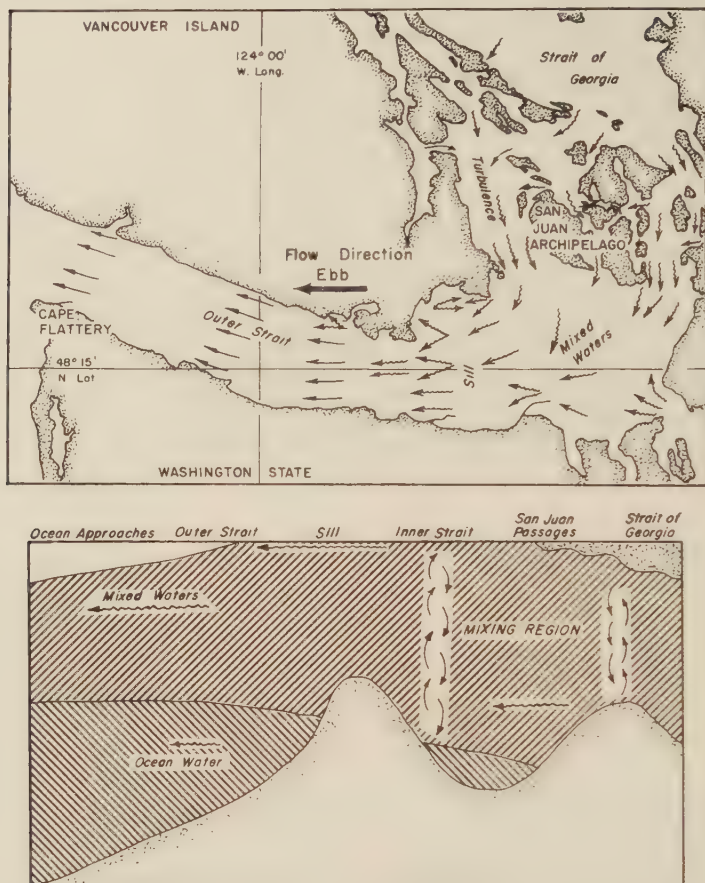


FIG. 40. Features of the ebb excursion of the flow in Juan de Fuca Strait and approaches.

is constrained along the mainland side. Back eddies and violent tide rips are formed in the approaches to Victoria. Evidently there is considerable lateral and vertical mixing in the Inner Strait and the waters approach homogeneity.

The near-surface part of the mixed waters in the Inner Strait move seaward over the sill. This must be so, because the outgoing flow is strongest near the surface, and there is no evidence in the structure that deep water from the Inner Strait crosses the sill (Fig. 11, 14, 23 and 28). However, because of the vertical constriction of the channel, there must be a submerged stream (wake stream) extending seaward from the sill.

In the Outer Strait the flow is reduced to the order of one knot at strength. The zone structure is re-established as the mixed waters over-run the dense ocean water, and are refreshed by the considerable land drainage. In this reach, the upper part of the double halocline (Fig. 15) represents the unaltered waters

from the Inner Strait. The lower part of the halocline is doubtless the result of entrainment of ocean waters in the wake stream at the sill.

The first of the seaward flow is almost entirely confined to the northern side, but as it strengthens it expands across the strait. When the seaward flow is fully developed the velocity distribution is nearly uniform, and the time of change to inward flow is first noticed on the southern side of the strait.

From the Outer Strait, the waters enter the ocean approaches which are, comparatively, a resting body of water. Here the discharge forms a wake stream (Tully, 1941) which veers to the right (Coriolis force) and is dissipated northward along the coast of Vancouver Island. This is illustrated by the calculated stream lines shown in Fig. 41.

This phenomenon occurs at the ocean outlet of each coast drainage system. Together these discharges create a geostrophic current flowing northward, close inshore, along the whole coastline north of the Columbia River (Latitude 46°N).

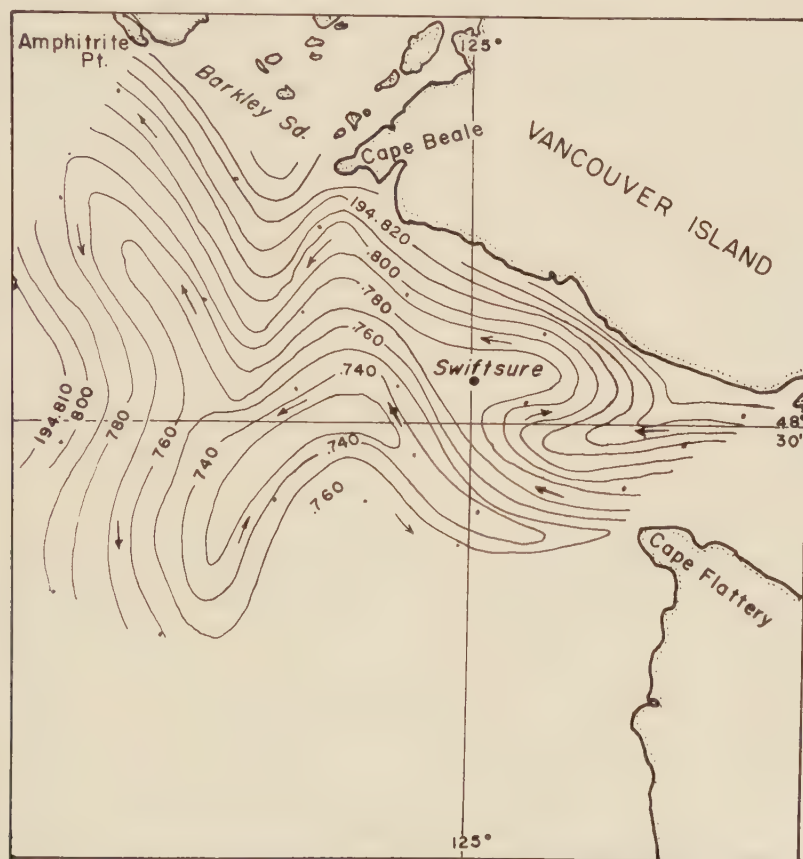


FIG. 41. Calculated stream lines in the approaches to Juan de Fuca Strait (after Tully, 1941).

EXCURSION

The mean tidal excursions in Herlinveaux's (1954) section (A, B, C) are shown in Fig. 42. These are representative of the Outer Strait.

The excursions of the surface water in Haro and Rosario Straits, determined from analyses of the data in Tidal Current Tables (U.S. Coast and Geodetic Survey, 1959) are shown in Table III.

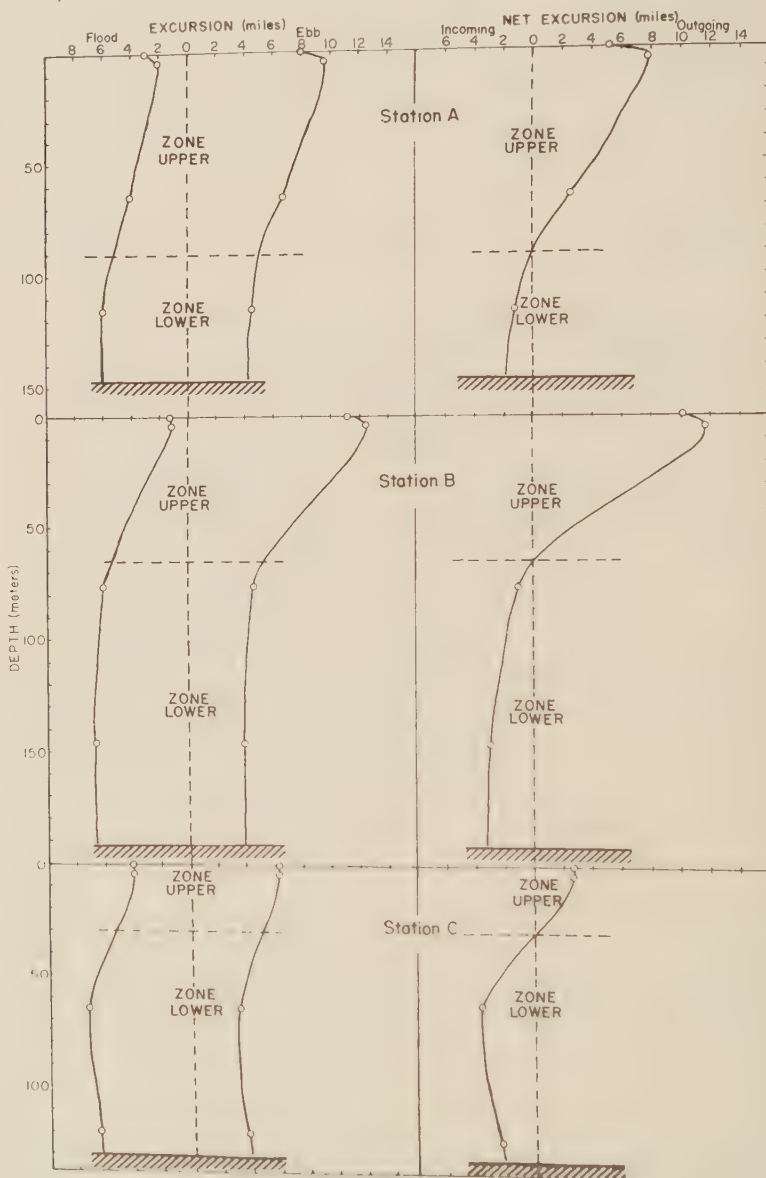


FIG. 42. Mean excursion of the flood (inward) and ebb (outward) through the section (A, B, C) in Juan de Fuca Strait (after Herlinveaux, 1954).

TABLE III. Surface water excursion in Haro and Rosario Straits, September 1960 (30 days = 29 tidal days). Calculated from tidal current data (U.S. Coast and Geodetic Survey, 1959).

	Haro	Rosario
	Flood (mean)	
Duration (minutes)	356.6	396.7
Mean speed (knots)	0.99	1.01
Excursion (nautical miles)	5.87	6.67
	Ebb (mean)	
Duration (minutes)	389.4	349.6
Mean speed (knots)	1.41	1.09
Excursion (nautical miles)	-9.15	-6.33
Net excursion (nautical miles)	Ebb 3.28	
	Flood	0.34

THE TIDAL PUMP

The mechanism in Juan de Fuca Strait (Fig. 38 and 40) is in effect a pump, the sill acting as a valve. During the ingoing flow, ocean water is transferred to the Inner Strait because the deep currents are stronger than those near the surface. This water is conserved near the bottom. It does not escape seaward during the ebb, because then the surface flow is the stronger and the weaker bottom flow is not sufficient to return the deep water seaward over the sill. Thus the intruding ocean water, brought in by the strong ingoing flow, cannot escape seaward and remains to be carried forward towards the Strait of Georgia on the next flood. The Inner Strait is a region of exchange. In effect, the water that reaches the Inner Strait from the Strait of Georgia is mixed to homogeneity and enriched with ocean water; part is returned to the lower zone of the Strait of Georgia, and the remainder escapes seaward. Undoubtedly, as proposed by Waldichuk (1957) this is the important mechanism for limiting the salt budget of the Strait of Georgia.

CONCLUSION

This report provides a factual overall description of the properties of the water, oceanographic structure, the current, and the variations and interrelations of these. It was designed and written to be a primary reference for ready use, and to provide a basis for more sophisticated discussions of particular features, which we trust will follow.

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Temporal Changes of Salinity, Temperature, and Dissolved Oxygen Content of the Water at Station "P" in the Northeast Pacific Ocean, and Some of Their Determining Factors¹

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ABSTRACT

Oceanographic data collected at Ocean Weather Station "P" (Lat. 50°N, Long. 145°W) during the 2 years between August 1956 and July 1958 are presented to show the principal features of the variations of salinity, temperature, and dissolved oxygen content of the water at the station. Probable factors influencing the water properties are discussed and explanations are given to account for these variations. Only those causing changes in the upper zone are discussed in detail.

There is good agreement between the observed changes of salinity in the upper zone and changes attributable to the effect of precipitation minus evaporation for the period summer through winter, 1956. However there is generally poor agreement for the rest of the period. The main factor influencing temperature in this zone is heat transfer at the air-sea boundary. Changes of dissolved oxygen content in this zone are governed primarily by changes of solubility of oxygen in water.

Horizontal transport of water in the locality influences the properties at the station appreciably. The general increase of salinity, temperature, and dissolved oxygen content that occurred during summer 1957 through summer 1958, is attributed to the northward transport of water. Transport, both from the region of the "dome" located northwest of the station, and from the west, also appears to influence the properties of water at the station during autumn and winter. Intense vertical mixing during autumn and winter affects the structure of water in the upper zone by redistributing the properties.

INTRODUCTION

SINCE the summer of 1955, the waters of the northeast Pacific Ocean region² have been examined by oceanographic surveys in summer and winter. These data have been reported (Fish. Res. Bd. Canada, 1956; 1957a; 1957c; 1958a).

In addition, oceanographic observations have been made regularly through alternate 6-week periods at Ocean Weather Station "P" (Lat. 50°N, Long. 145°W) (Fig. 1) since August 1956. The details of the cruises associated with these observations are shown in Table I. Data collected here have been reported (Fish. Res. Bd. Canada, 1957b; 1958b; 1959) and some aspects of the data discussed (Tabata, 1960). These data reveal many features of the temporal variations of the properties of water at this fixed position. Furthermore, they provide data of sufficient continuity so that it is possible to interpret some of the sequences of oceanographic events that have occurred in the region between the periods of the major surveys.

¹Received for publication May 23, 1961.

²Hereafter, the northeast Pacific Ocean region bounded by Lat. 40°N and Long. 180°W, and the coast of North America will be referred as "the region", unless ambiguity results.

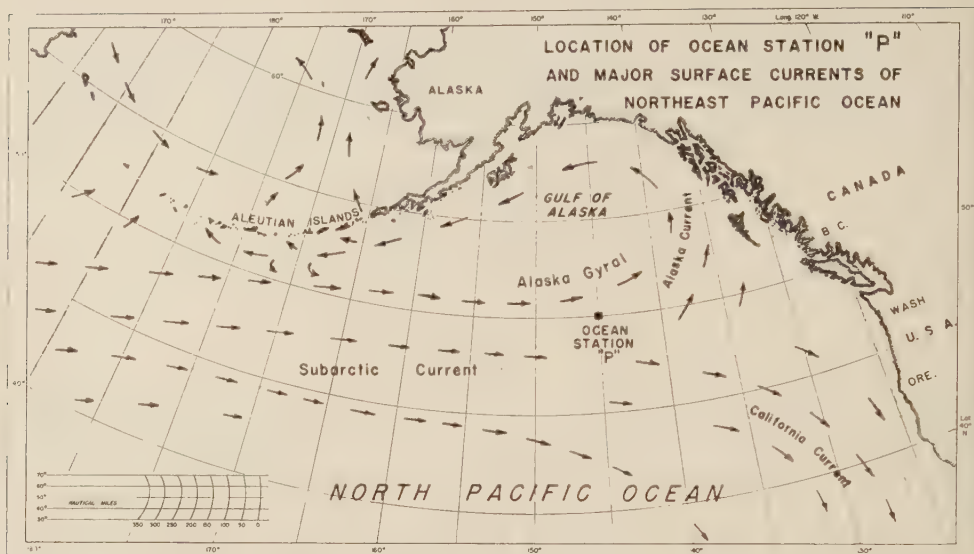


FIG. 1. Chart showing location of Ocean Weather Station "P" and major surface ocean currents of Northeast Pacific Ocean.

TABLE I. Catalogue of cruises during which observations were made.

Cruise number	Dates	Number of hydrographic stations occupied	Number of days between mid-dates of cruises
P-56-1	25 August–26 September 1956	7	—
P-56-2	10 November–7 December 1956	4	74
P-57-1	27 January–2 March 1957	8	83
P-57-2	20 April–29 May 1957	12	86
P-57-3	13 July–21 August 1957	11	84
P-57-4	28 September–29 October 1957	10	73
P-57-5	14 December 1957–22 January 1958	12	81
P-58-1	9 March–16 April 1958	11	84
P-58-2	31 May–8 July 1958	12	84

GENERAL OCEANOGRAPHIC FEATURES OF THE EASTERN SUBARCTIC WATER

The general features of the Eastern Subarctic Water have already been discussed by several authors (Doe, 1955; Tully and Dodimead, 1957; Dodimead, 1958; Bennett, 1959). As some aspects of these have bearing on the fluctuations of oceanographic properties at Station "P", they are briefly reviewed here.

The main feature of the salinity structure of this Water in the region is the presence of an upper zone (0–100 m), a halocline (100–200 m), and a lower zone (>200 m). As shown in Fig. 2, the upper zone is characterized by a relatively low-salinity water (32.7‰). In winter, the water in this zone is mixed to homogeneity, and hence the salinity in the zone is constant (Fig. 2a). However, in summer, an appreciable vertical salinity gradient is present in the zone as shown in Fig. 2b. The halocline represents a transitional zone between the upper and the lower zone. Here, the salinity increases markedly with depth, by as much as 1.0‰ within an interval of 100 m. The lower zone represents the layer in which the salinity increases gradually with depth. From a value of about 33.8‰ at the

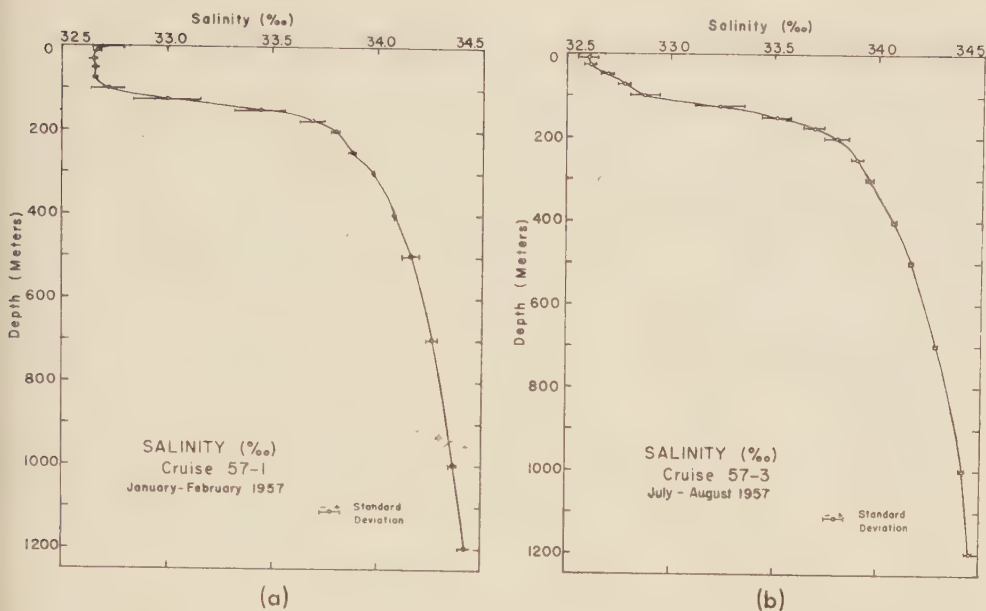


FIG. 2. Salinity-depth profiles for water at Station "P" (mean values for each cruise).
(a) Winter. (b) Summer.

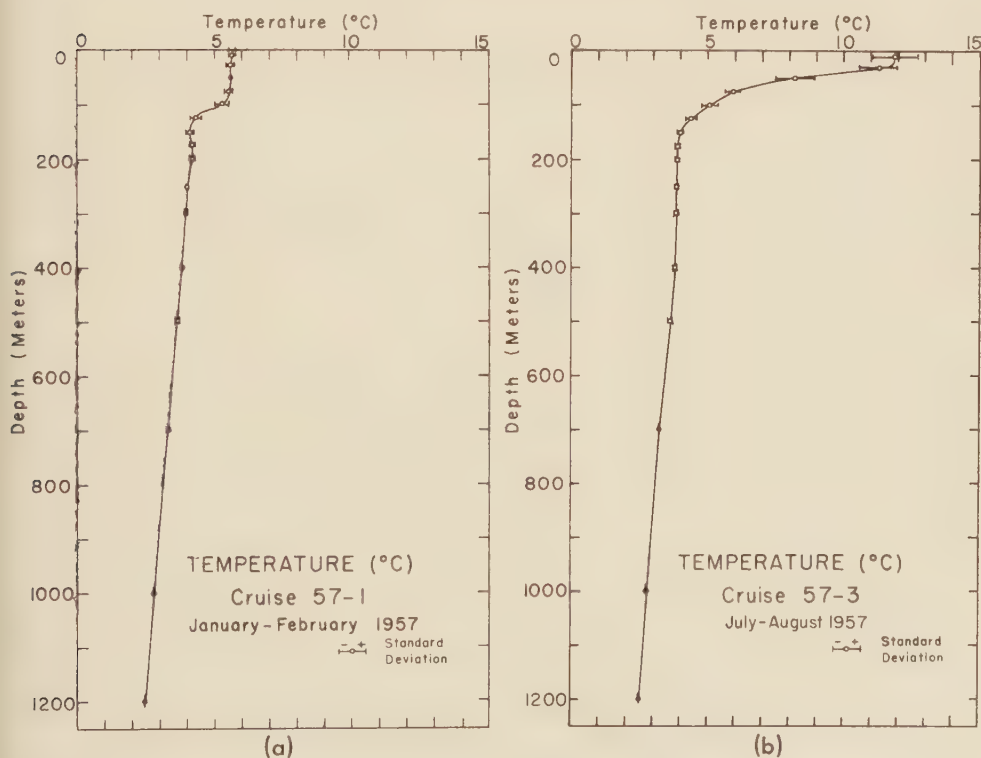


FIG. 3. Temperature-depth profiles for water at Station "P" (mean values for each cruise).
(a) Winter. (b) Summer.

bottom of the halocline, the salinity increases to 34.4‰ at a depth of 1000 m, and finally to 34.7‰ near the ocean bottom.

The water in the upper zone is isothermal in winter, as shown in Fig. 3a. However, in summer, a well-defined thermocline occurs in the zone (Fig. 3b) where the temperature may decrease with depth by as much as 8 °C within an interval of 20 m. In the halocline, the temperature generally decreases with depth (Fig. 3b). But occasionally, a temperature inversion (temperature increasing with depth) occurs, as shown in Fig. 3a. In the lower zone, the temperature decreases gradually with depth, reaching 2.8°C at a depth of 1000 m, and finally 1.5°C near the ocean bottom.

These three zones can be identified conveniently by reference to the three segments of the temperature-salinity (T-S) curve shown in Fig. 4.

The dissolved oxygen content (hereafter called the oxygen) in the upper zone is generally constant (0.63 milligram atoms per litre (mg-at/l)) in winter, as shown in Fig. 5a. But in summer (Fig. 5b) the oxygen increases with depth in the zone from a value frequently less than 0.6 mg-at/l at the surface to a maxi-

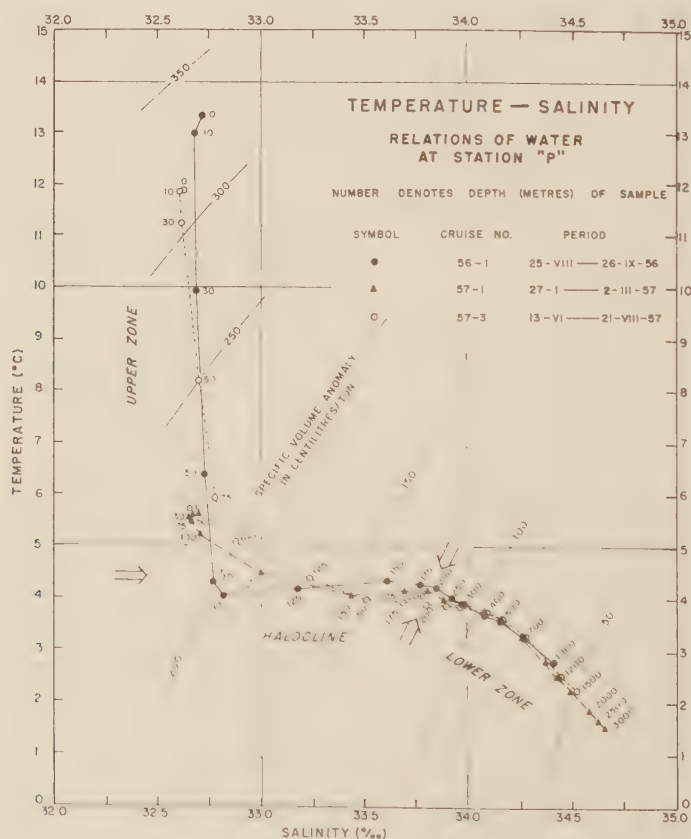


FIG. 4. Temperature-salinity relations of water at Station "P". (Mean values for each depth, for each cruise, have been plotted. Large arrows indicate limit of various zones.)

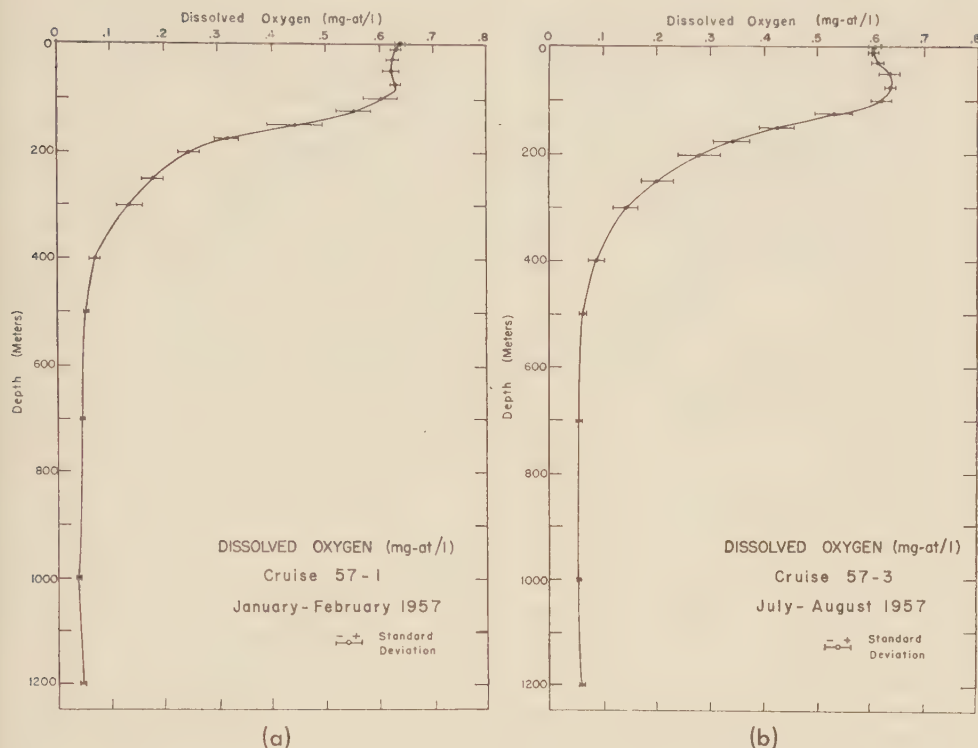


FIG. 5. Dissolved oxygen content-depth profiles for water at Station "P" (mean values for each cruise). (a) Winter. (b) Summer.

imum (0.63 mg-at/l) at depths between 50 and 100 m. It decreases markedly in the halocline, reaching 0.3 mg-at/l at the bottom of the halocline. It then decreases gradually in the lower zone to a minimum of less than 0.05 mg-at/l at depths varying from 200 to 1200 m (between 500 and 1200 m at Station "P"). From this minimum it increases gradually with depths to 0.3 mg-at/l near the ocean bottom.

To the south of the Subarctic Water lies the Subtropic Water. The Subarctic Boundary separates these two water masses. Its location has been determined by Dodimead (1958) and is shown in Fig. 6. At the longitude of Station "P", the boundary lies about 400 miles³ south of the station. The Subtropic Water is more saline and warmer than the Subarctic Water. It has been shown (Tully and Dodimead, 1957; Dodimead, 1958) that the Subtropic Water lacks the characteristic halocline of the Subarctic Water and possesses a salinity minimum at depths ranging from 200 to 600 m. Furthermore the Subtropic Water has no major temperature inversion. In Fig. 7 are shown the T-S characteristics of these water masses. Being so close to this boundary, the characteristics of this Subtropic Water still have some of the features characteristic of the Subarctic Water. For instance, there is a remnant of a halocline between the depths of 100 and 200 m.

³All horizontal sea distances expressed in miles in this paper are nautical miles (1.85 km).



FIG. 6. Chart showing the location of Subarctic Boundary and stations occupied during the major surveys (Dodimead, 1958).

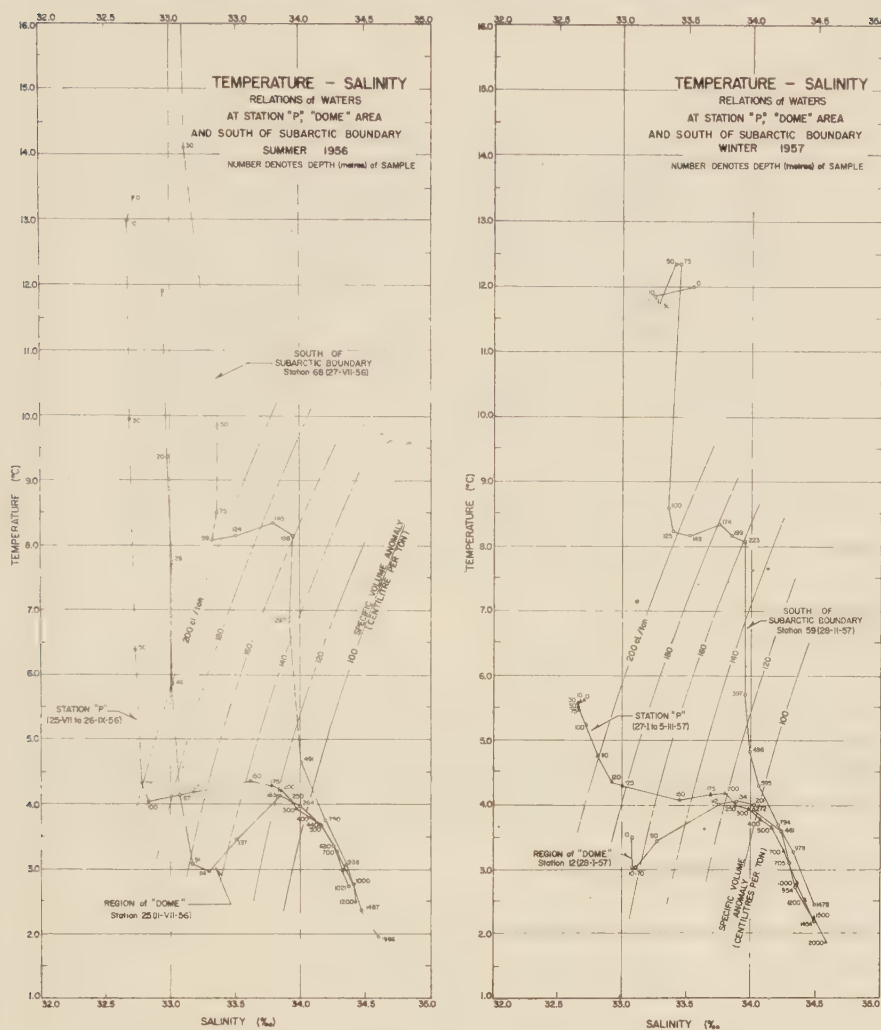


FIG. 7. Temperature-salinity relations of waters near the Subarctic Boundary, in the "dome" area, and at Station "P" (for location of stations, see Fig. 6).

Northwest of Station "P" lies the "dome"⁴. It is characterized by having water of relatively higher salinity (Fig. 8-10), lower temperature (Fig. 11-13) and lower oxygen (Fig. 14-16), than is present in the immediate surroundings. This feature of salinity and temperature of the "dome" water is verified in the T-S curve as shown in Fig. 7.

A comparison of the geopotential topographies which represent the currents (Fig. 17), with the distributions of salinity (Fig. 8-10), temperature (Fig. 11-13), and oxygen (Fig. 14-16), indicates that the "dome" lies in the centre of the counter-clockwise circulation system of the Alaska Gyral (Fig. 1).

⁴The term "dome" is used since the isometers of all properties on sections drawn through the cold centre of the Gulf of Alaska are dome-shaped.

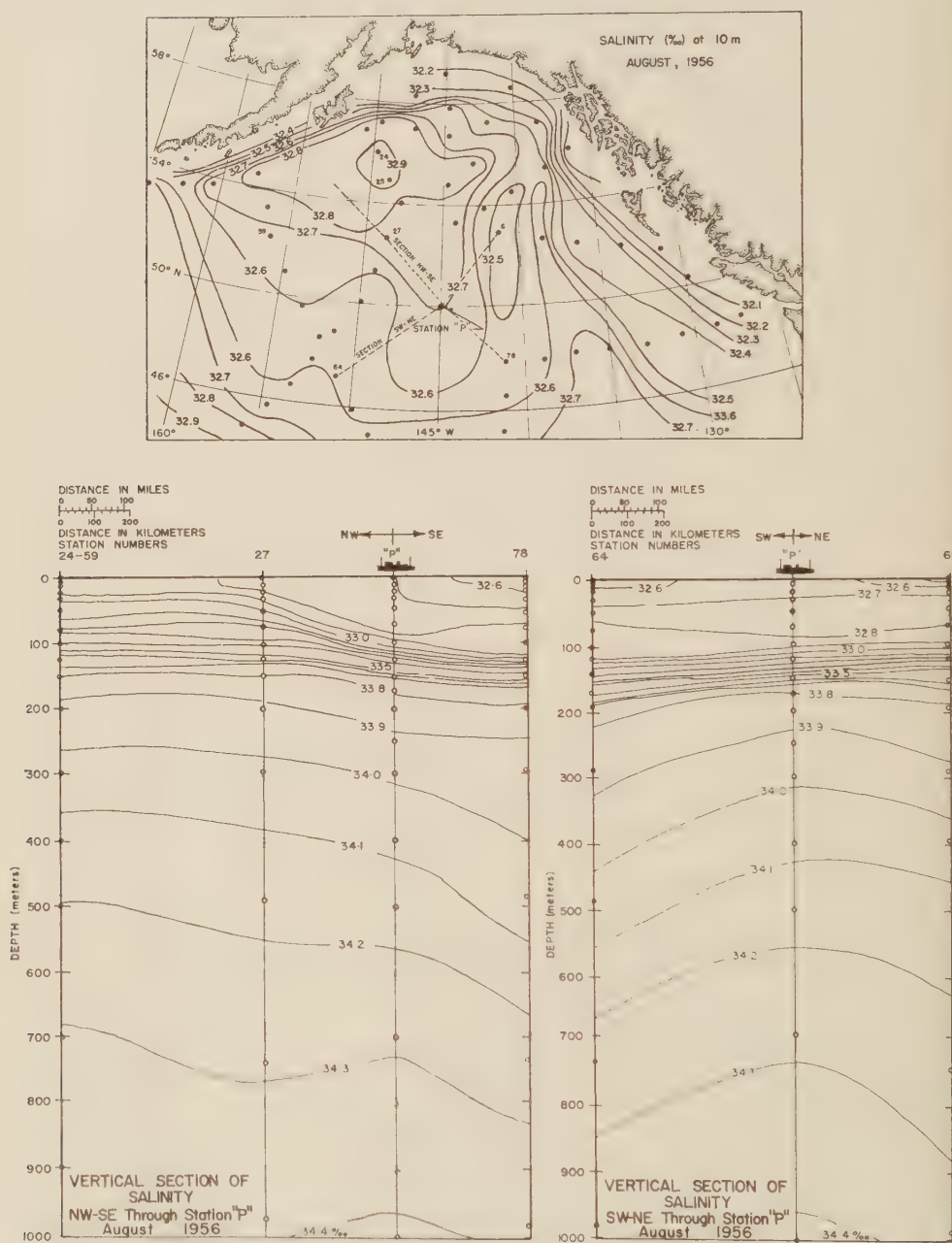


FIG. 8. Salinity, Summer 1956. *Upper*—Lateral distribution of salinity at depth of 10 m. *Lower*—Distribution of salinity in vertical sections.

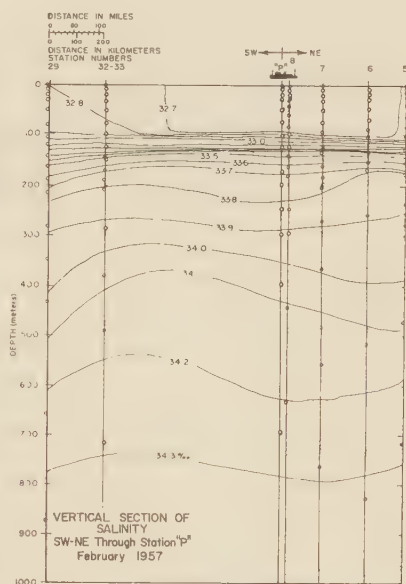
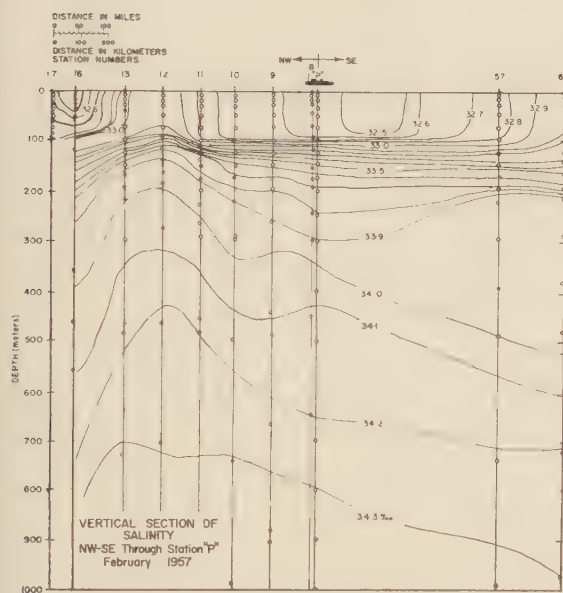
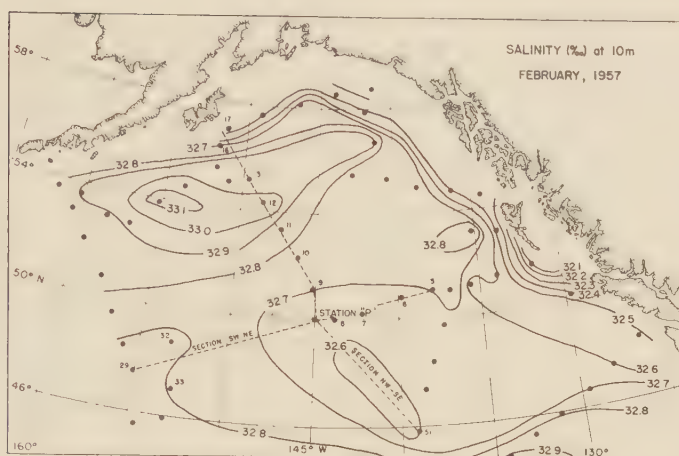


FIG. 9. Salinity, Winter 1957. *Upper*—Lateral distribution of salinity at depth of 10 m. *Lower*—Distribution of salinity in vertical sections.

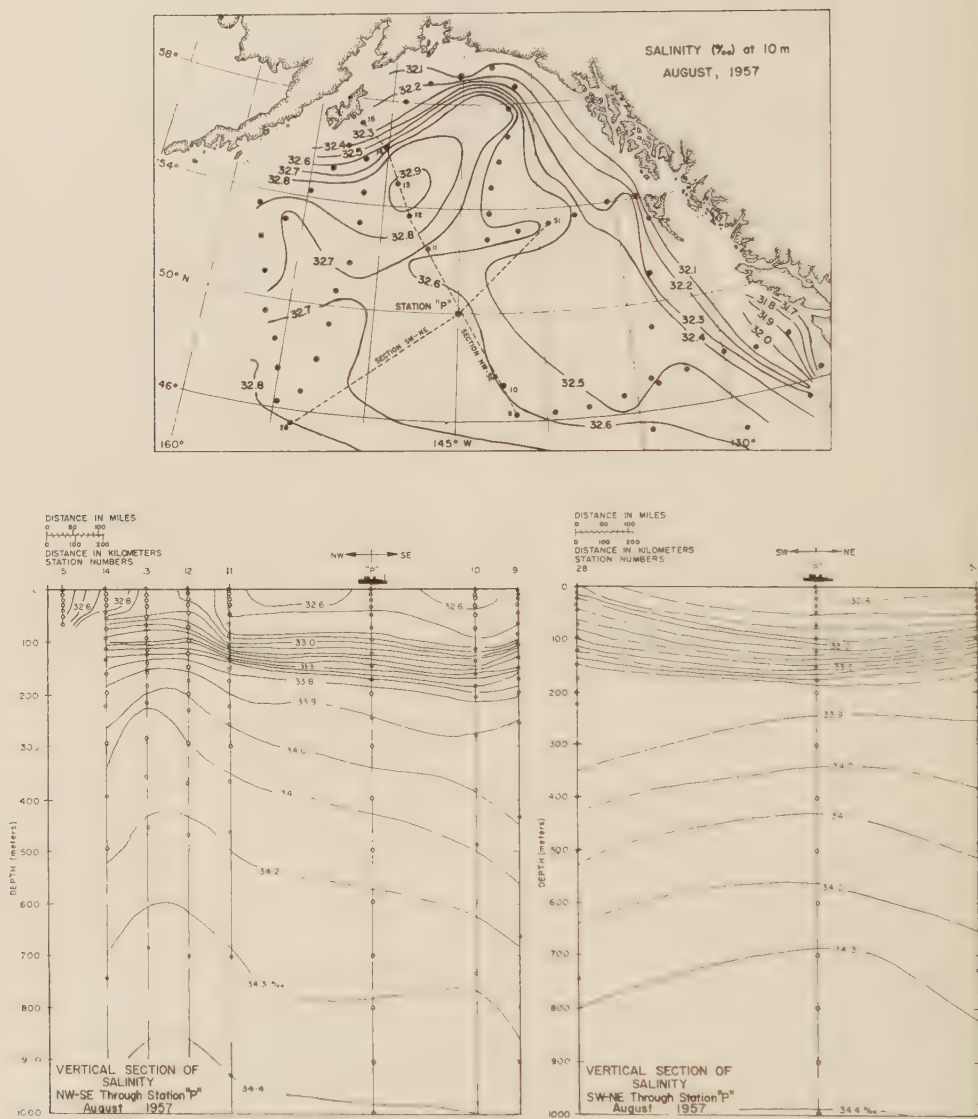


FIG. 10. Salinity, Summer 1957. *Upper* Lateral distribution of salinity at depth of 10 m. *Lower*—Distribution of salinity in vertical sections.

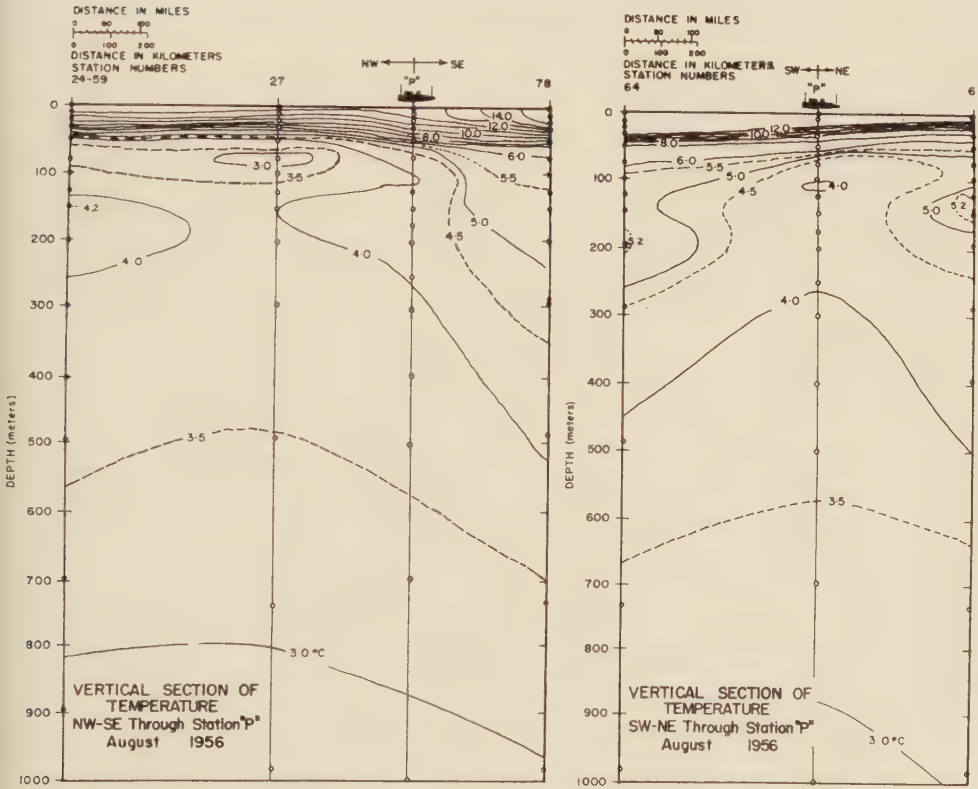
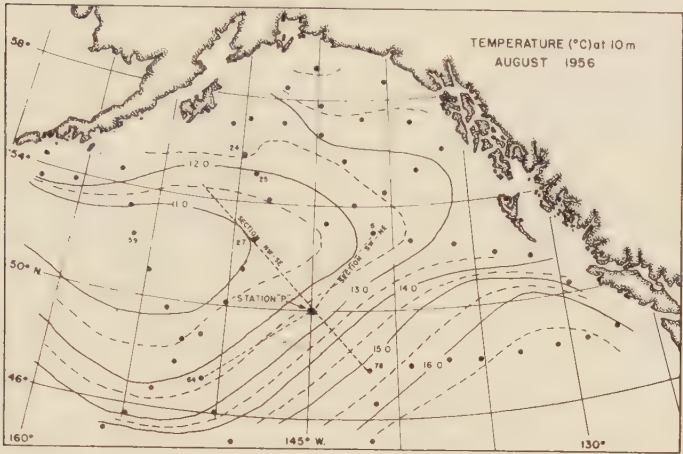


FIG. 11. Temperature, Summer 1956. *Upper*—Lateral distribution of temperature at depth of 10 m. *Lower*—Distribution of temperature in vertical sections.

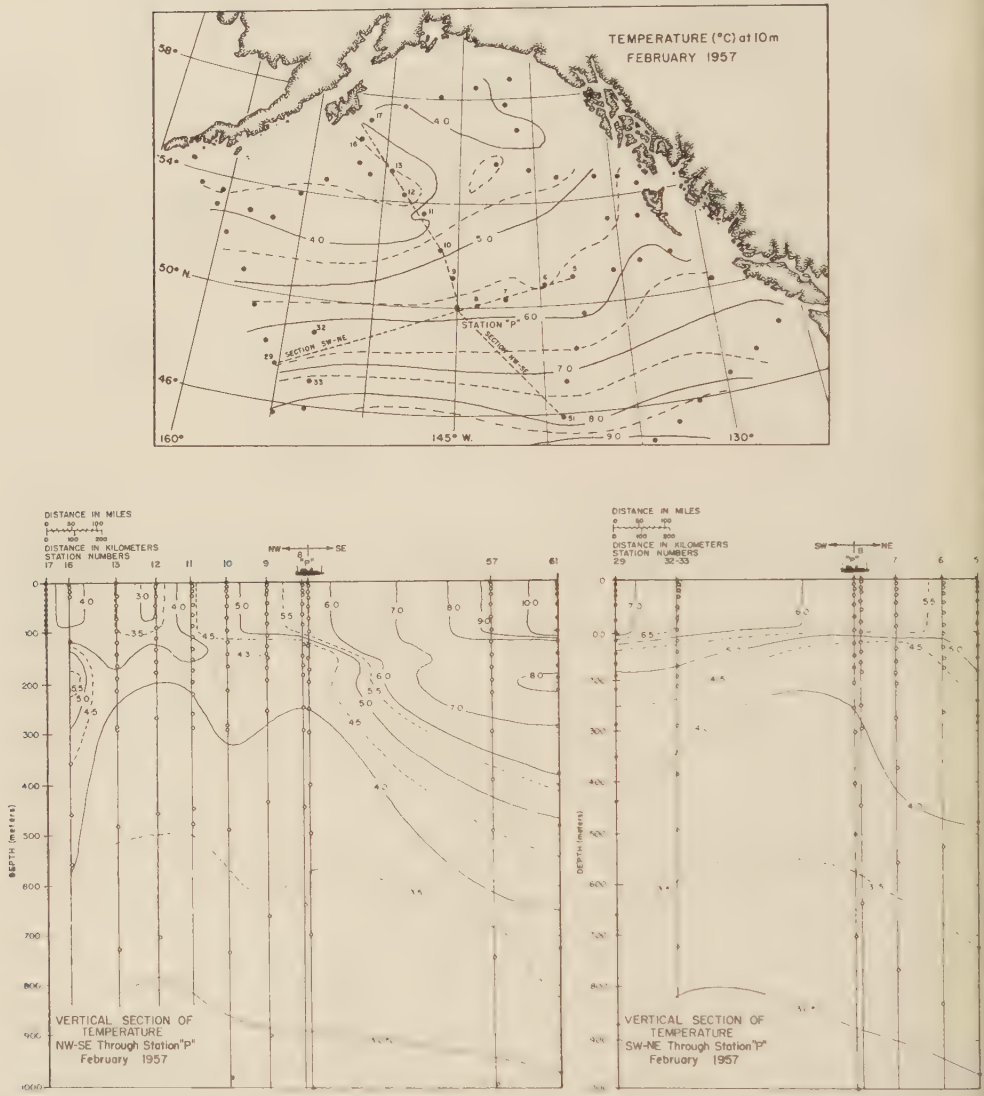


FIG. 12. Temperature, Winter 1957. *Upper*—Lateral distribution of temperature at depth of 10 m. *Lower*—Distribution of temperature in vertical sections.

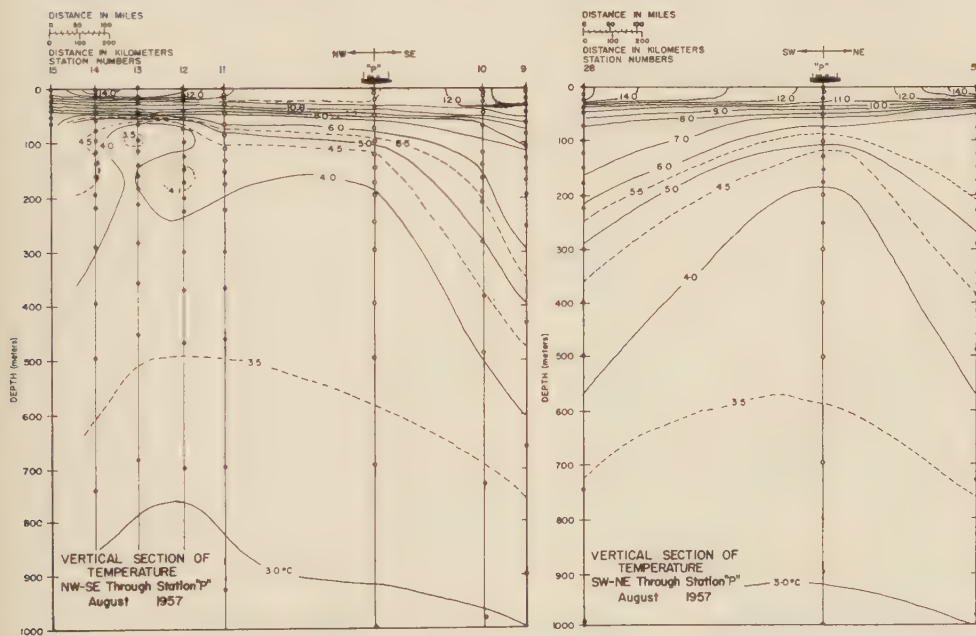
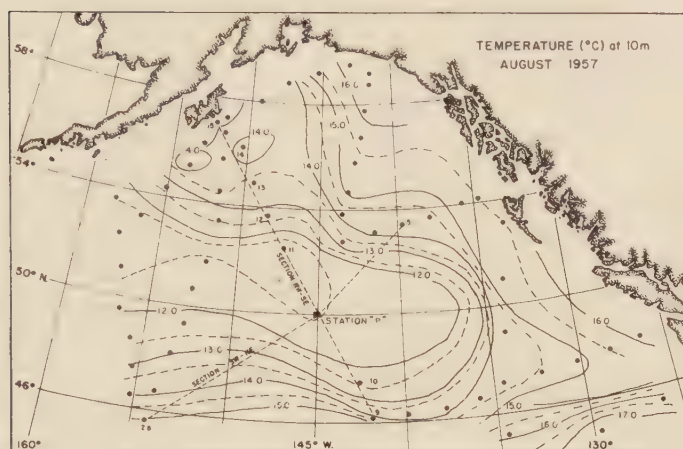


FIG. 13. Temperature, Summer 1957. *Upper*—Lateral distribution of temperature at depth of 10 m. *Lower*—Distribution of temperature in vertical sections.

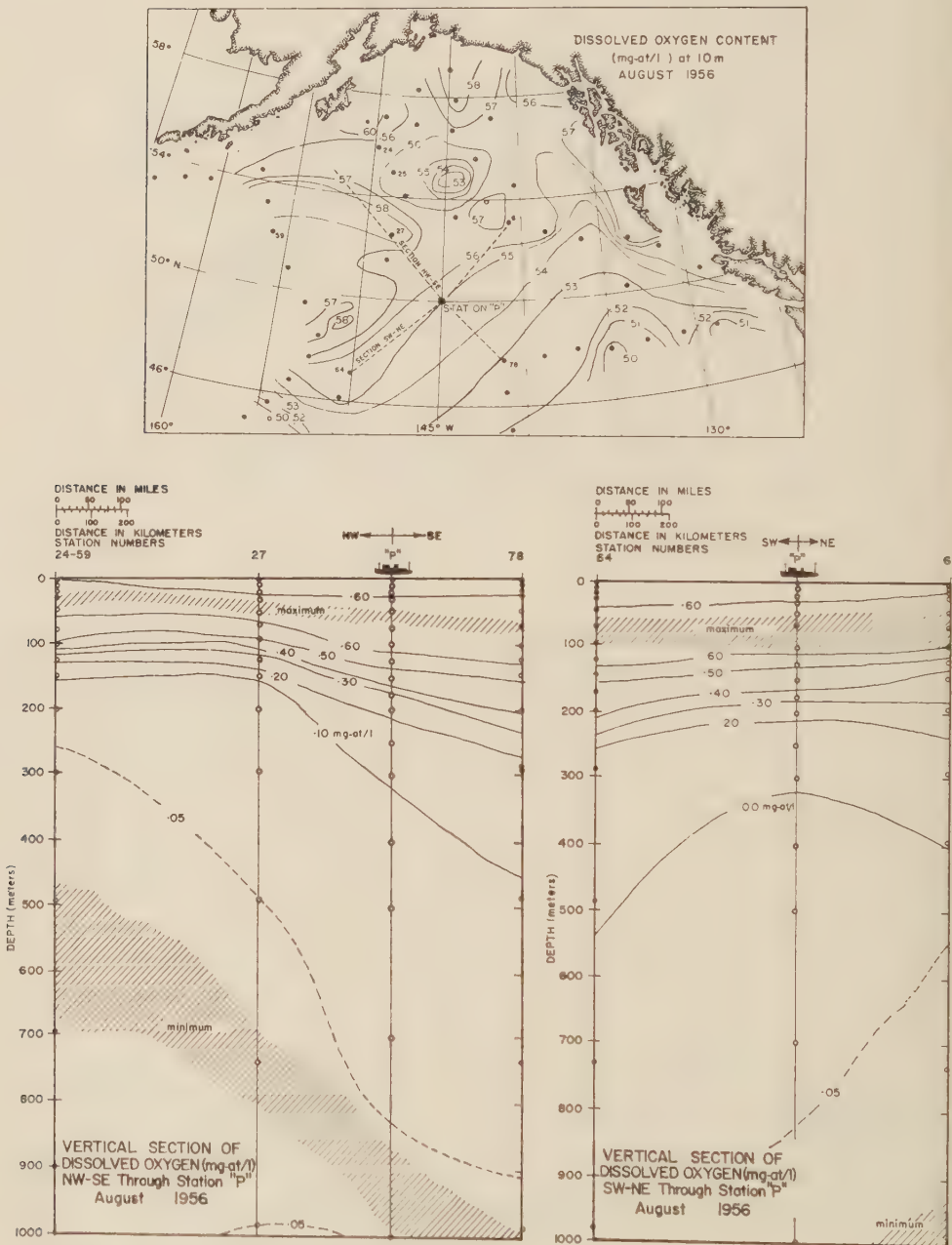


FIG. 14. Dissolved oxygen content, Summer 1956. *Upper*—Lateral distribution of dissolved oxygen content at depth of 10 m. *Lower*—Distribution of dissolved oxygen content in vertical sections.

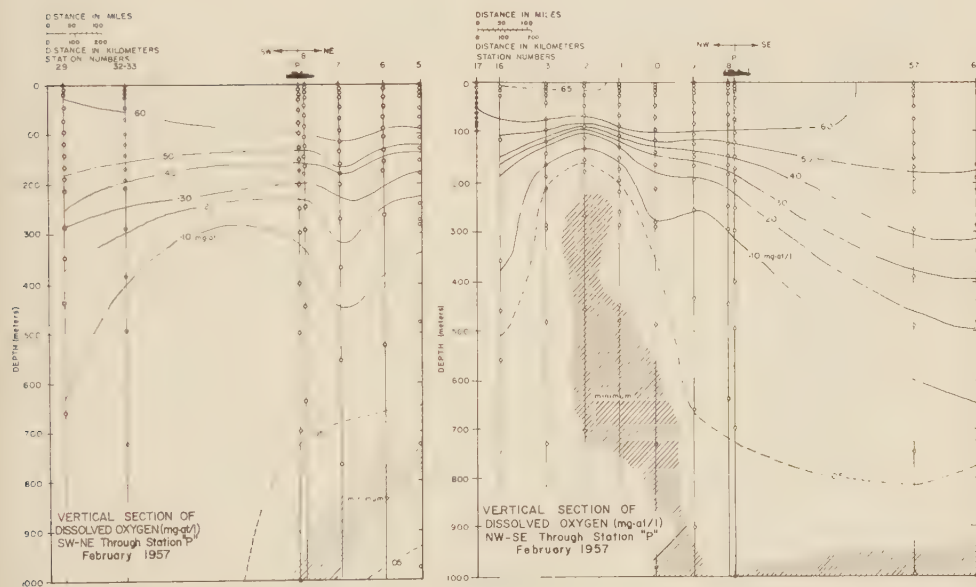
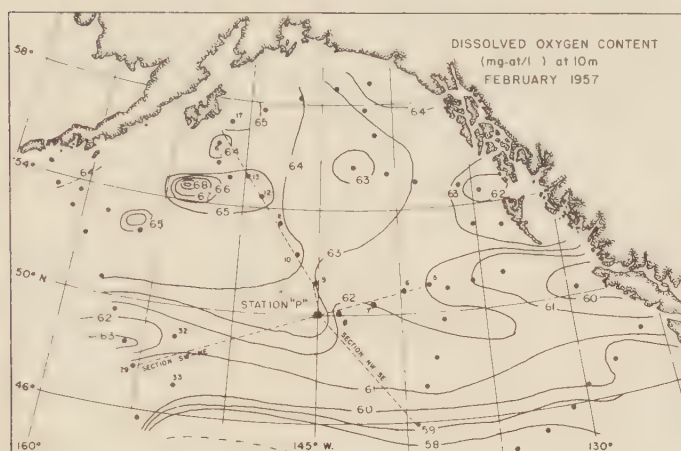


FIG. 15. Dissolved oxygen content, Winter 1957. *Upper*—Lateral distribution of dissolved oxygen content at depth of 10 m. *Lower*—Distribution of dissolved oxygen content in vertical sections.

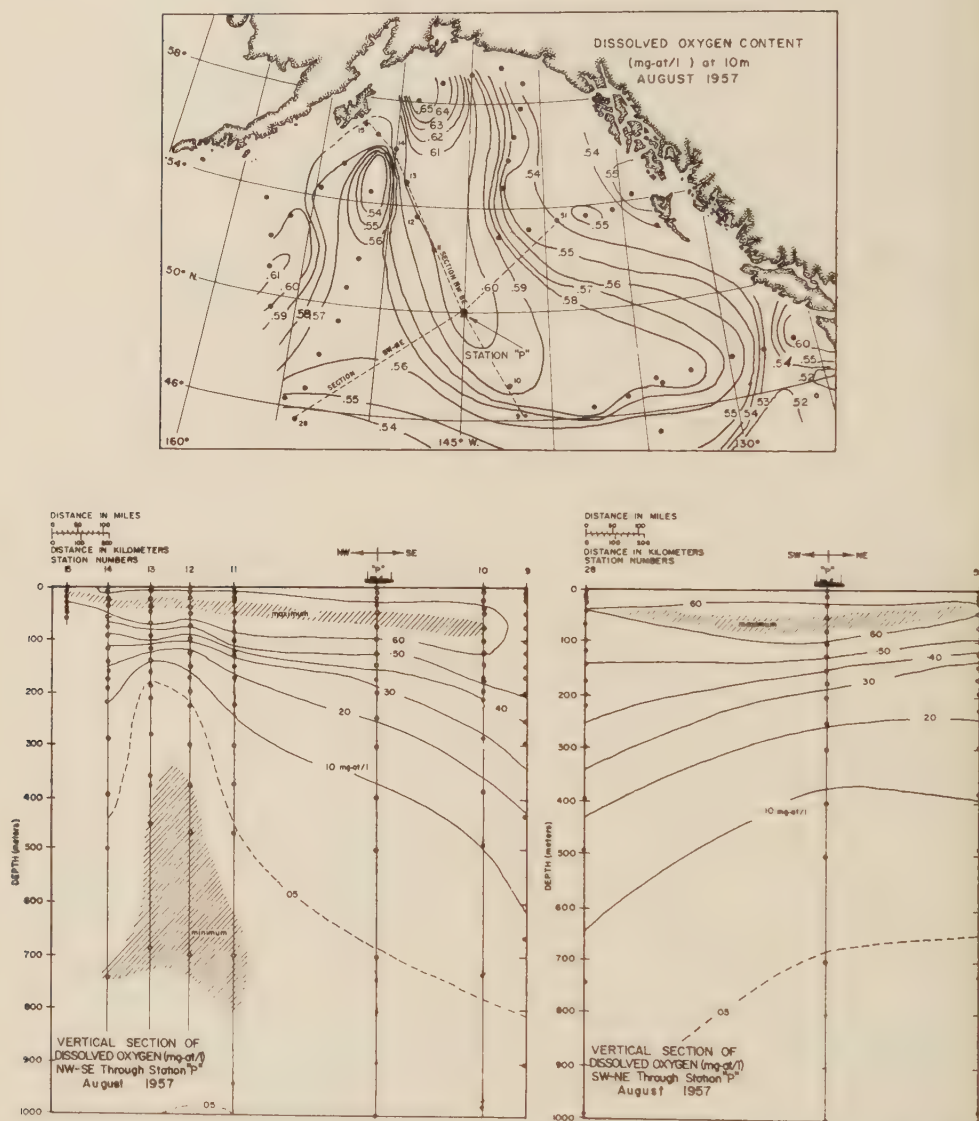


FIG. 16. Dissolved oxygen content, Summer 1957. *Upper*—Lateral distribution of dissolved oxygen content at depth of 10 m. *Lower*—Distribution of dissolved oxygen content in vertical sections.

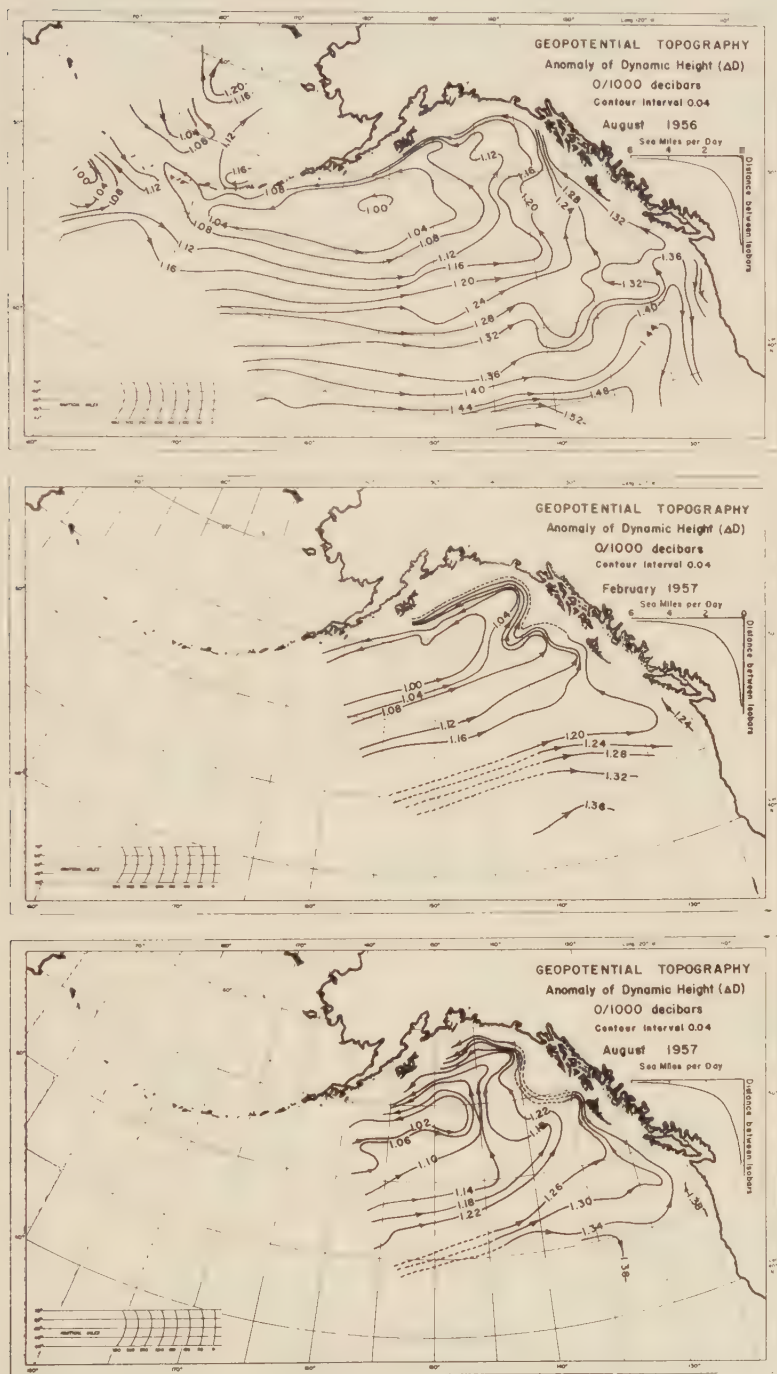


FIG. 17. Geopotential topography (referred to 1000 decibars) for North-east Pacific Ocean. *Top*—Summer 1956. *Middle*—Winter 1956/57. *Bottom*—Summer 1957. (Dodimead, 1958.)

In order to show the distributions of the properties of water at Station "P" relative to those of the surroundings, vertical sections of these properties are drawn (Fig. 8-16). A comparison of these sections of salinity, temperature, and oxygen through this station indicates that the most pronounced horizontal gradients are in the direction northwest to southeast. This is particularly noticeable with the gradient of oxygen.

The Subarctic Current flows westward across the north Pacific Ocean (Sverdrup *et al.*, 1942) until it approaches the coast of North America. Here it divides to form the northward-flowing Alaska Current and the southward-flowing California Current (Fig. 1). Station "P" lies in the path of this near-zonal Subarctic Current where it changes its course northward. It lies well within the region of the Subarctic Water but is between the well-defined "dome" water to the northwest, and the Subtropic Water to the south.

VARIATIONS OF SALINITY

In Fig. 18 A and B are shown the seasonal values of salinity of the water at Station "P" for the 2 years between August 1956 and July 1958. The same data are plotted in three different ways to facilitate the presentations. The variations of salinity are most marked in the upper zone and in the halocline, and are less marked in the lower zone. Noticeable variations occur at all depths to at least 1000 m (Fig. 18A *upper* and *lower*). However, the annual range of salinity in the lower zone is about an order less than that in the upper zone (Tabata, 1960).

There is little evidence of cyclic annual variations of salinity in the upper zone, except perhaps at a depth of 100 m where the salinity reaches a maximum in autumn and decreases to a minimum in winter. In five of the eight intervals between the cruises, the changes in the halocline are in phase with those in the upper zone (Fig. 18A, *upper*; Table II). During the remainder of the time, they are in opposite phase. Although the magnitudes of the variations in the lower zone are smaller than those in the upper zone and the halocline, there appears to be some phase agreement between them. Moreover, 50% of the time there is a good phase agreement between the variations in all three zones (Table II).

FACTORS INFLUENCING SALINITY

In the discussion to follow, factors associated with air-sea boundary processes are discussed first. This is followed by comments on horizontal transport (advection) and finally on other factors. Similar introductory remarks also apply later to the discussions on factors influencing temperature and oxygen.

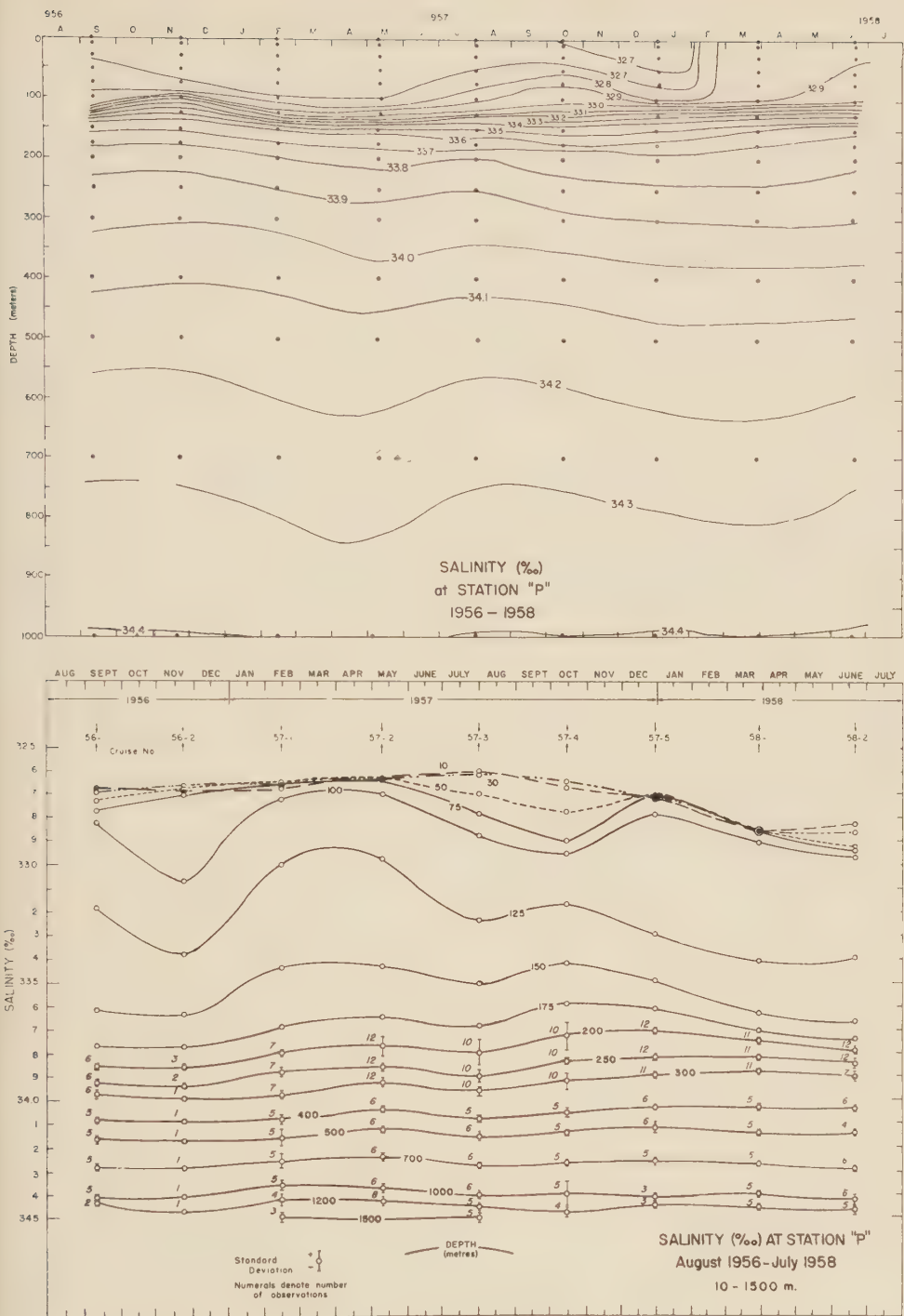


FIG. 18A. Salinity at Station "P", Summer 1956–Summer 1958. (The data over the approximate 6-week period are combined and plotted as a single point. This corresponds to observations at mid-date of the cruise period.) Upper—Seasonal distribution of salinity (0–1000 m). Lower—Seasonal values of salinity at depths: 0, 10, 30, 50, 75, 100, 125, 150, 175, 200, 250, 300, 400, 500, 700, 1000, 1200, and 1500 m.

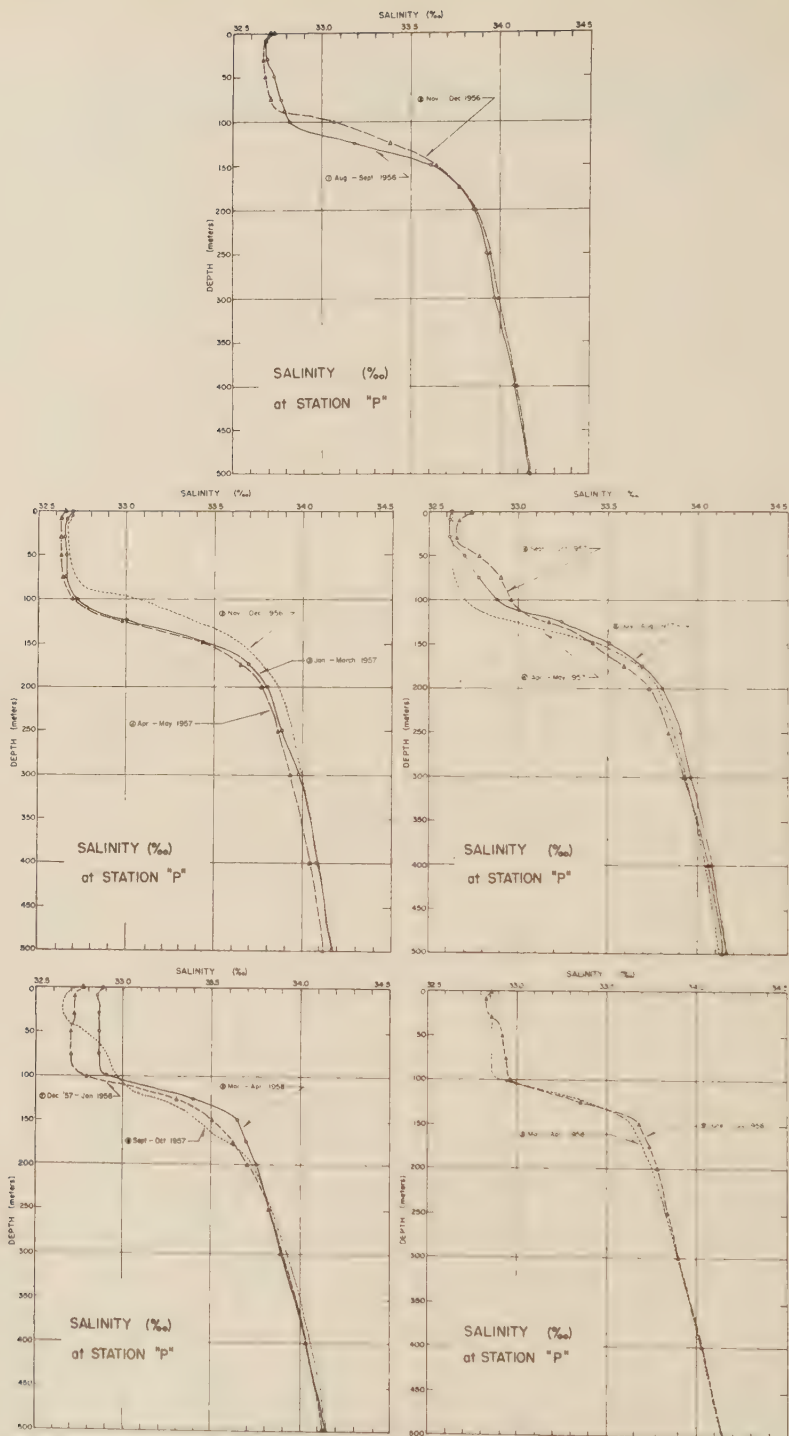


FIG. 18B. Salinity at Station "P", Summer 1956-Summer 1958. Vertical profiles of salinity (0-500 m).

FRESH WATER EXCHANGE ACROSS THE AIR-SEA BOUNDARY: PRECIPITATION AND EVAPORATION

The surface water of the ocean becomes diluted or concentrated, depending on whether or not fresh water is added or taken away. Dilution in the open ocean is accomplished by precipitation in the form of rain, snow, and hail, and to a very small extent by the condensation of water vapour above the sea surface. Concentration, on the other hand, is accomplished by evaporation of fresh water from the sea surface. Therefore, fresh water exchange across the air-sea boundary due to precipitation and evaporation is the most important factor influencing the salinity of the surface water. In the northeast Pacific Ocean, its influence is said to be confined primarily to the water above the halocline (Tully and Barber, 1960).

Jacobs (1951) indicated that in this region there is usually an excess of precipitation (P) over evaporation (E) throughout the year. For instance, in the general vicinity of Station "P", the excess of precipitation over evaporation fluctuates from a maximum (20 cm/season) in autumn to a minimum (10 cm/season) in winter. He further indicated that this excess generally increases to landward from the vicinity of that station to the coast of Alaska, British Columbia, and Washington, and decreases to westward and to southward. However, in the immediate neighborhood of the station, say within a radius of 100 miles, the values of this excess are relatively uniform, according to the charts prepared by him.

The monthly mean values of precipitation (unpublished meteorological record data, 1958, Meteorological Services of the Department of Transport, Canada), evaporation (calculated from Formula (6a) of the present paper), and $P-E$ at Station "P" are shown in Fig. 19. It is evident from this Figure

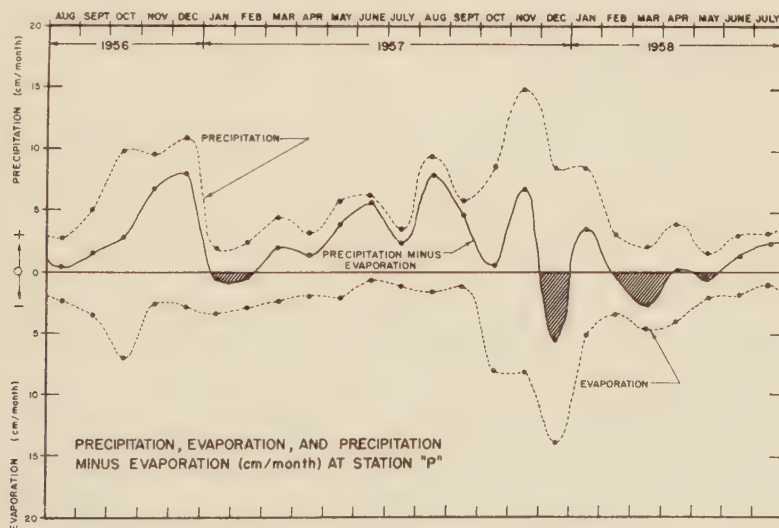


FIG. 19. Monthly mean values of precipitation, evaporation, and precipitation minus evaporation ($P-E$) at Station "P", Summer 1956–Summer 1958. (By $P-E$ is meant the difference of precipitation and evaporation where precipitation and evaporation have *positive* values.)

that precipitation generally exceeds evaporation during all seasons except in winter.

The change of salinity, ΔS due to $P - E$, during the time interval Δt may be evaluated from the formula:

$$\Delta S = S_f - S_i \simeq -S_i \left(\frac{P - E}{z} \right) \quad \dots \dots (1)$$

where: S_f is the final salinity (‰),

S_i is the initial salinity (‰),

z is the depth (cm) of column considered (upper zone), and

$P - E$ is the difference of precipitation and evaporation in centimetres during the time interval Δt .

At Station "P", the salinity of the upper zone is about 32.7‰. Thus, given a value of $P - E$ of 10 cm, the salinity of the upper zone (0-100 m) would decrease by 0.03‰, a magnitude of change well within the detectable limits. (Precision of salinity determinations at 35‰ level is ± 0.004 ‰ at 0.05 probability level (Strickland and Parsons, 1960) when determinations are made with UW-PNL conductivity bridge (Paquette, 1959).)

The observed seasonal changes of salinity in the upper zone and also those changes that could result from the effect of seasonal variations of $P - E$ are shown in Table II. Comparison of these changes indicates that through summer

TABLE II. Observed seasonal changes of salinity in upper zone (0-100 m), precipitation minus evaporation ($P - E$), and effect of $P - E$ in changing the salinity in upper zone.

Seasons:	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Cruise No.:	56-1	56-2	57-1	57-2	57-3	57-4	57-5	58-1	58-2
Increase (+) or decrease (-) of salinity:									
Upper zone (0-100 m)	-	-	-	+	+	-	+	+	+
Halocline (100-200 m)	+	-	-	+	-	+	+	+	+
Lower zone (>200 m)	+	-	-	+	-	-	negligible	+	+
Observed change of salinity (‰/month) in upper zone:									
	-0.014	-0.019	-0.007	+0.023	+0.032	-0.033	+0.054	+0.020	
Precipitation minus evaporation (cm/month):									
	+3.71	+4.75	+1.03	+3.94	+4.34	+5.01	-0.081	-1.31	
Salinity change (‰/month) in upper zone that can be accounted for by effect of $P - E$:									
	0.014	-0.016	-0.003	-0.013	-0.013	-0.016	+0.003	-0.011	

and winter of 1956, the decrease of salinity in the upper zone could be almost wholly accounted for by dilution from excess of precipitation. During the first part of 1957, about 50% of the decrease could be accounted for by dilution. But from spring 1957 through summer 1958 (except for the decrease that occurred between autumn and winter 1957), the salinity increased despite the excess precipitation.

HORIZONTAL TRANSPORT

Transport of water from regions of different properties could cause changes in the properties at any fixed position.

If it can be assumed that vertical currents, vertical and horizontal mixing, and effects of divergence and convergence are negligible compared to horizontal currents (in the present discussion these are assumed to be negligible to the first approximation) then the influence of currents in changing the property of water may be expressed by:

$$\frac{ds}{dt} = v \frac{ds}{dx} \quad (2)$$

where: s is any conservative concentration such as salt or heat,

$\frac{ds}{dt}$ is the change of concentration per day,

v is the current speed in kilometres per day, and

$\frac{ds}{dx}$ is the gradient of concentration parallel to the direction of the current in units of concentration per kilometre.

The effects of transport at certain periods are discussed only at the periods when data from adjacent regions are available.

The general increase of salinity in the upper zone and halocline during spring 1957 through summer 1958 is attributed to the northward transport of water. The water lying to the south of Station "P" is usually more saline than in the vicinity of the station (Tully and Dodimead, 1957; Dodimead, 1958). Hence, a northward transport of this water would tend to increase the salinity at the station. From the consideration of the horizontal salinity gradients (Fig. 10, *upper*) and surface currents (Fig. 17, *bottom*) for August 1957, it is estimated, from Equation (2), that due to this effect, an increase of salinity at the rate of 0.040‰/month occurred. This transport effect, plus that due to P-E, gives the observed increase of salinity for summer 1957 (Table II), and it is probable that a similar situation also occurred at other periods, except during autumn to winter, 1957. This northward transport is consistent with the anomalous warming of water in the northeast Pacific Ocean during the corresponding period, a phenomenon attributed to the intrusion of warm southern water into the region (Namias, 1959; Tully *et al.*, 1960; Sette and Issacs, 1960).

The decrease of salinity that occurred in the upper zone during autumn through winter, 1957, is due partly to dilution (Table II). The remainder is attributable to the transport of less-saline water from the west or northwest direction. The manner in which this transport might have occurred could be explained from the shift of winds in the region. In Fig. 21 (*upper*) is shown the usual atmospheric pressure system over the northeast Pacific Ocean. Figure 21

(lower) shows the system that occurs occasionally in autumn and winter, as in October 1956 and December 1957. The westerly winds associated with this latter system are indicated in Fig. 20. It is probable that, due to these westerly winds, the less-saline water frequently lying to the west or northwest of Station "P" during the summers (Tully and Dodimead, 1957; Dodimead, 1958) was driven into the vicinity of the station by drift currents associated with these winds.

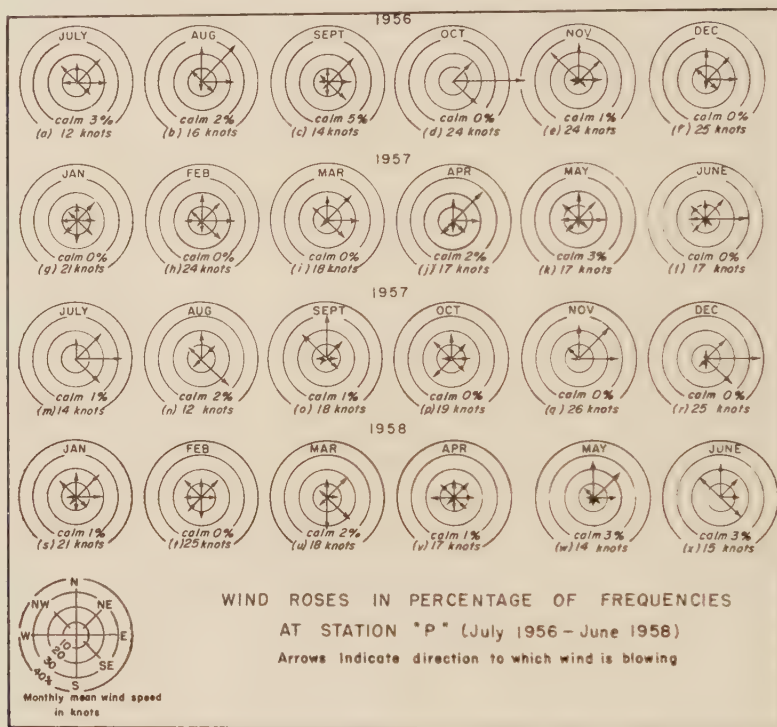


FIG. 20. Wind rose in percentage of frequencies and mean monthly wind speed at Station "P", Summer 1956–Summer 1958.

The increase of salinity in the halocline and lower zone during summer through autumn, 1956, appears to have been due to transport of the relatively saline water from the northwest, particularly from the vicinity of the "dome". It is only in the direction of the "dome" that the water at these levels is more saline than at Station "P" (Fig. 8, lower left), and southward transport of the water from this direction could account for the increase.

Conversely, the decrease that occurred at these levels during autumn through winter, 1956, is probably due to the northward transport of water, since it is in the southerly direction that relatively low salinity water presumably occurred, as in summer 1956 (Fig. 8, lower).

While the salinity increased in the halocline and the lower zone between summer and autumn, 1956, it decreased at these levels during the corresponding

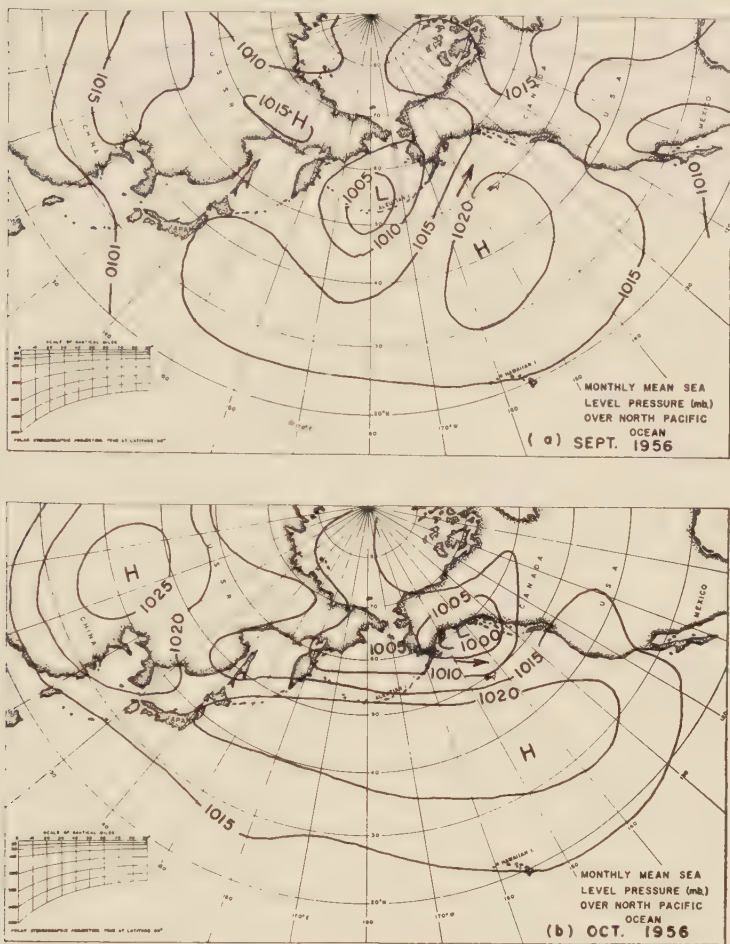


FIG. 21. Monthly mean sea level pressure charts for North Pacific Ocean. *Upper*—September 1956. *Lower*—October 1956. (Extended Forecast Section, U.S. Weather Bureau.) (December 1957 chart is similar to that for October 1956.)

period in the following year, 1957. This decrease is perhaps due to the transport of less-saline water from the south (Fig. 10, *lower*).

Any salinity change that is common to all three zones, as shown in the above example, is associated with transport of the entire column of water in the same general direction. This is consistent with the conclusion made by Bennett (1959), who pointed out that geostrophic currents occur to a depth of at least 1000 m, and that they flow in the same general direction as the surface current.

VERTICAL MIXING

Since the effect of fresh water exchange due to precipitation and evaporation is confined primarily to the immediate surface layer of the ocean, it is necessary

to examine the process of vertical mixing⁵ by which this effect is distributed into the deeper layers. To illustrate how this mixing affects the structure of the properties of the water in the upper zone, Fig. 22 depicts the progressive deepening of the mixed-layer depth (bottom of the homogeneous layer). The thickness of the homogeneous layer reflects the extent to which the vertical mixing is effective in redistributing the properties of water. The manner in which mixing alters the structures may be seen in more detail from the comparison of the structures, as shown in Fig. 23.

At present, the exact mechanism of this mixing is not well understood. Presumably it is due to the combination of two processes, one associated with winds and the other associated with evaporation.

Winds may promote mixing by their accompanying effects such as stirring due to wave actions, wind-generated helical currents (Langmuir, 1938), and vertical turbulence associated with shear in the drift current (Ekman, 1905; Rossby and Montgomery, 1935). Comparison between the occurrence of strong winds in autumn and winter (Fig. 20) and the thickening of the homogeneous layer during this period (Fig. 22) suggests that winds are influential in causing mixing.

The effect of evaporation in initiating mixing is perhaps easier to understand than that of the winds. By continuously evaporating fresh water from the sea surface and by cooling, the surface water becomes denser than the water lying immediately below. As a result, the surface water sinks until it encounters water of the same density. The end result is that convection currents are set up and overturning of water occurs. Provided evaporation is large enough, this overturning could penetrate to great depths, as in the Mediterranean Sea where such a process causes convection currents to reach the bottom (Sverdrup *et al.*, 1942). As shown in Fig. 19, the evaporation is large in autumn and winter. Comparison of these periods and those of the deepening of the mixed-layer depth (Fig. 22) suggests that the large evaporation period is associated with period of this mixing.

It is sufficient to state here that there is an apparent relation between the winds and evaporation, and mixing. And as stated earlier, by such mixing redistribution of properties occurs. As is evident from Fig. 23, the salinity of the surface water increases while that immediately below decreases. Similarly, the temperature of the surface water decreases while the temperature of the layer immediately below increases. If $P-E=0$, then the gain of salt in the surface layer should equal the loss of salt in the layer below (i.e. the shaded area should equal the hatched area in Fig. 23).

The increase of salinity in the upper 50 m, and a part of the decrease that occurred below 50 m during autumn through winter, 1957, are both attributed to vertical mixing. Also, the occurrence of minimum annual salinity at a depth of 100 m in winter is believed to be due to this mixing.

⁵The term "vertical mixing" used here is associated with the autumnal breakdown of the structure of properties in the upper zone.

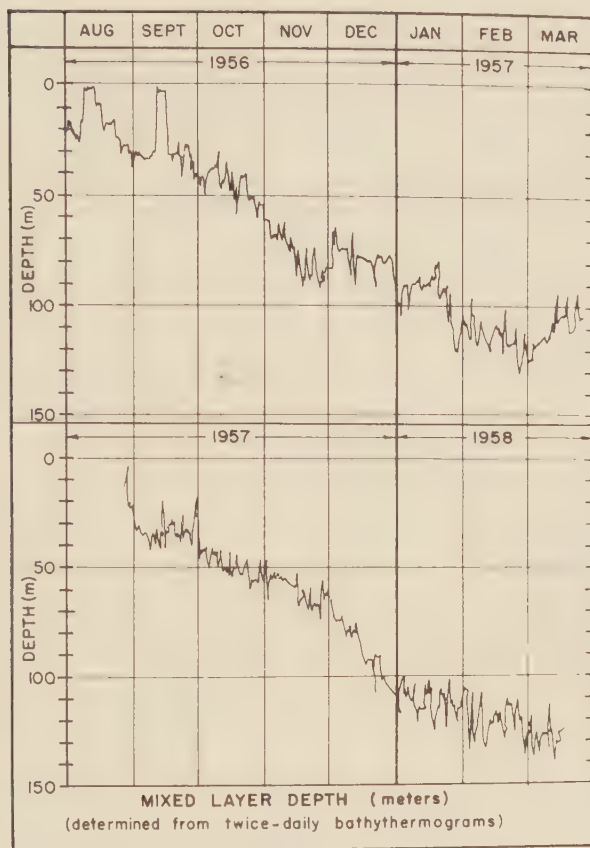


FIG. 22. Progressive deepening of the mixed-layer depth (thickness of homogeneous layer).

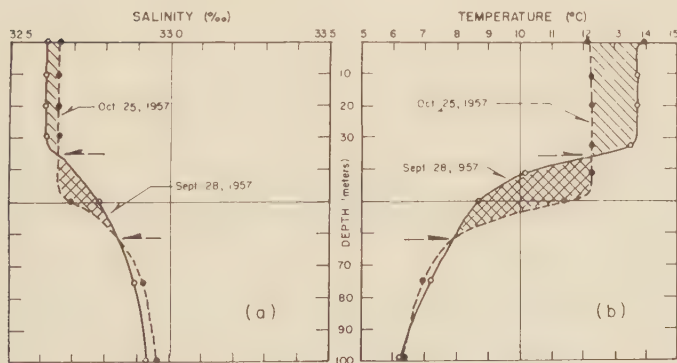


FIG. 23. Alteration of structures of properties of water due to vertical mixing.

OTHER FACTORS

Lateral and vertical eddy diffusion of salt may also affect the salinity at Station "P" if there are large lateral and vertical salinity gradients present in the locality, and if the magnitudes of the eddy coefficients are sufficiently large. Unfortunately, no data are available concerning the magnitudes of these coefficients. However, there are appreciable horizontal gradients of salinity in the vicinity of the station, as shown in the upper panels of Fig. 8, 9 and 10. In the summer of 1956 (Fig. 8, *upper*) the water at the station was almost surrounded by water of salinity less than that at the station. A horizontal eddy system in the vicinity would tend to decrease the salinity at the station under such conditions. There are no data to support this assumption of lateral eddy diffusion, but the possibility remains.

As shown earlier (Fig. 2 and 18A, *upper*), a fairly large salinity gradient occurs between the upper and lower zones throughout the year. As diffusion of salt proceeds from large concentration to lesser concentration, it follows that there must be a continuous upward transfer of salt across the halocline due to vertical eddy diffusion. This would tend to make the upper zone progressively more saline with time. But due presumably to the dilution from excess precipitation, the upper zone is prevented from becoming more saline. In a recent paper, Tully and Barber (1960) postulated the upward transport of salt across the halocline by entrainment, a process which occurs in estuarine waters (Tully, 1949). It is probable that this entrainment (a special type of eddy diffusion process) probably contributes to the upward transport of salt and may increase the salinity of the upper zone. But to what extent this process affects the salinity has not been ascertained.

Wind-induced divergences and convergences of water (Hidaka, 1955; Hidaka and Akiba, 1955) may also affect the structure of properties, the former by upwelling and the latter by "piling-up" of water. Although there is no proof, the atmospheric low-pressure area that prevailed over Station "P" during February 1958 may have resulted in local upwelling. The somewhat large salinity increase that occurred during this period may have been partly due to this effect.

VARIATIONS OF TEMPERATURE

The annual cycles of surface sea temperatures at Station "P" for the years 1956, 1957, 1958, and for the mean period 1950-1958, are shown in Fig. 24. The salient feature of the annual cycle is that the maximum (13-14°C) generally occurs in the late summer, and the minimum (5-6°C) in late winter. From the comparison of the 8-year means with the temperatures for the individual years, it is evident that the temperature in autumn and winter, 1956, is less than the corresponding long-term means, but that for spring 1957 through summer 1958 is consistently higher. This latter period coincides with the period of anomalous warming of water in the northeast Pacific Ocean (Namias, 1959; Tully *et al.*, 1960).

Two annual cycles of air and surface sea temperature are shown in Fig. 25. On comparing these cycles, it is evident that the major features of the two are

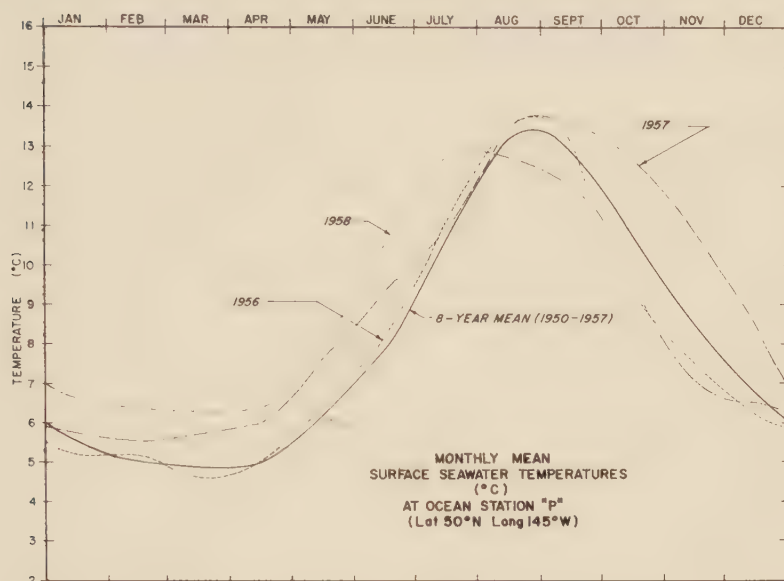


FIG. 24. Monthly mean surface sea temperature at Station "P", January 1956–December 1958, together with grand monthly means (1950–1957).

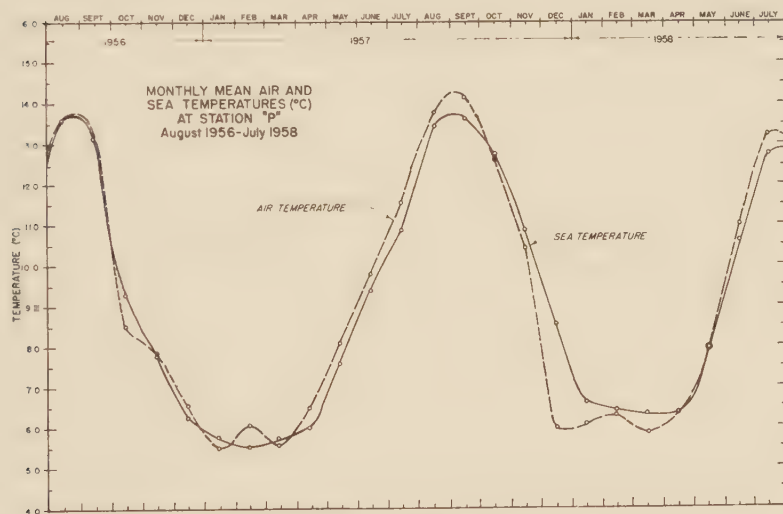


FIG. 25. Monthly mean values of air and sea temperature at Station "P", Summer 1956–1958 Summer.

similar. But in the winter the cycle of air temperature is more irregular than that of the sea temperature. Pickard and MacLeod (1953) showed that the shore water along the Canadian Pacific coast is warmer than the air in autumn and winter. Such a relation does not appear to hold at Station "P". In fact, during autumn and winter, 1956, the air was warmer than the sea.

The temperature of the subsurface water at Station "P" is shown in Fig. 26A and 26B. Marked annual variations occur at the surface and to a depth of

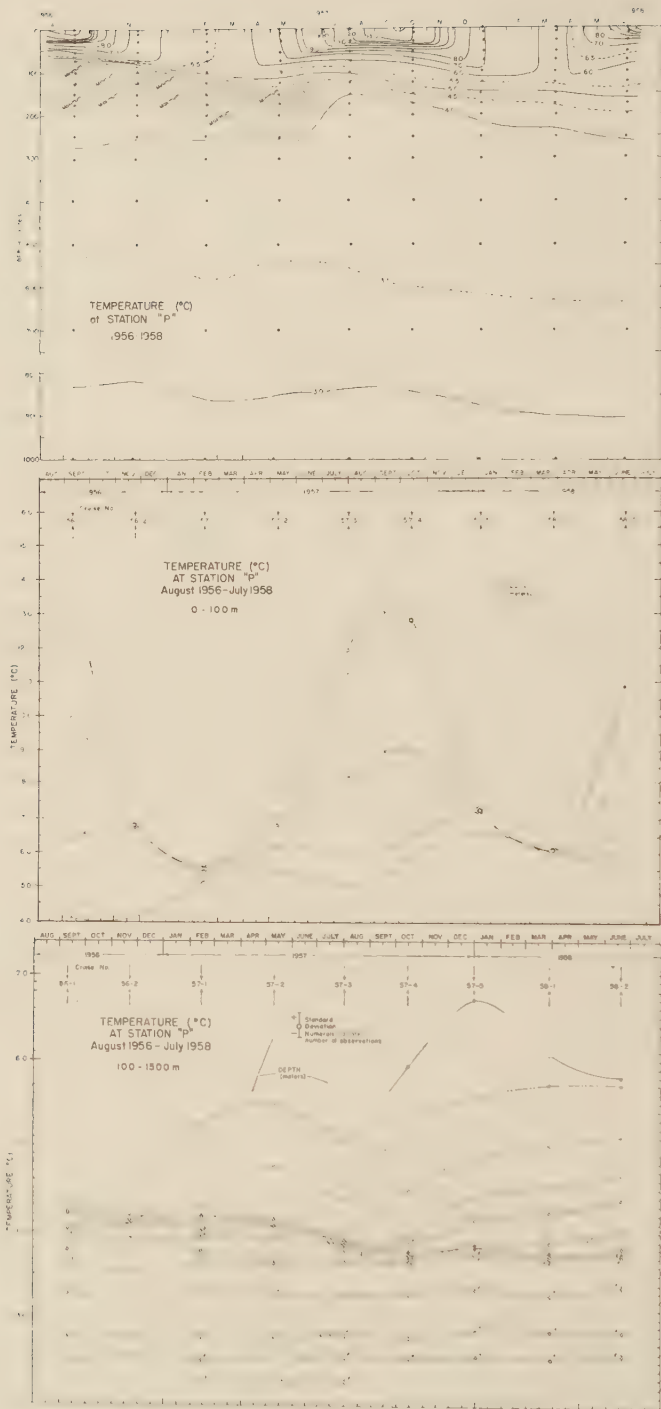


FIG. 26A. Temperature at Station "P", Summer 1956-Summer 1958. (The data over the approximate 6-week period are combined and plotted as a single point. This corresponds to observations at mid-date of the cruise period.) *Top*—Seasonal distribution of temperature (0-1000 m). *Middle*—Seasonal values of temperature at depths: 0, 10, 30, 50, 75, and 100 m. *Bottom*—Seasonal values of temperature at depths: 100, 125, 150, 175, 200, 300, 400, 500, 700, 1000, 1200, and 1500 m.

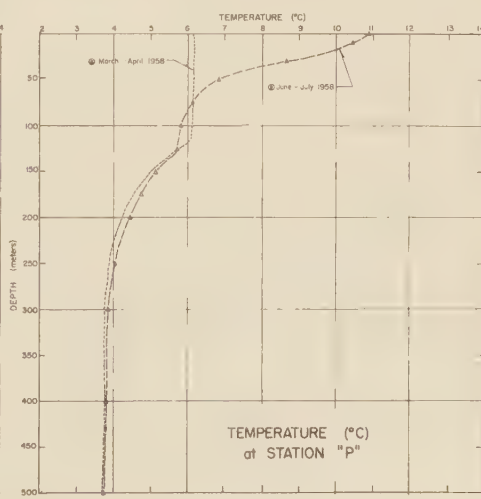
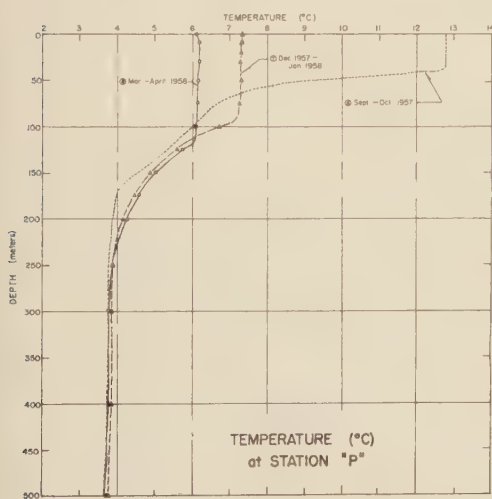
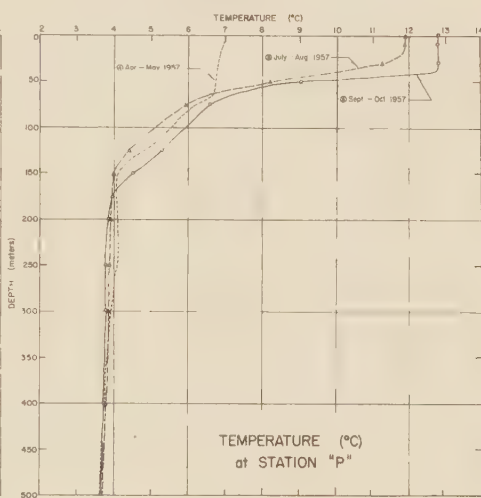
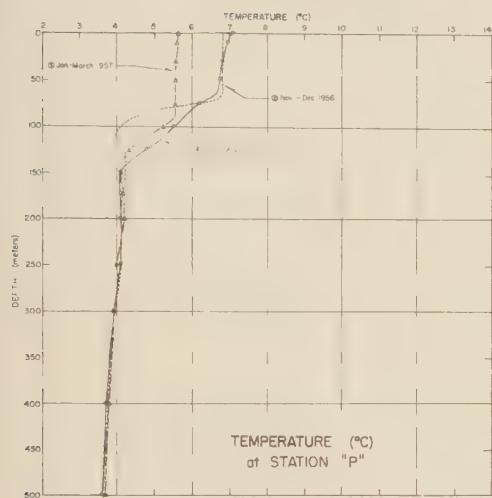
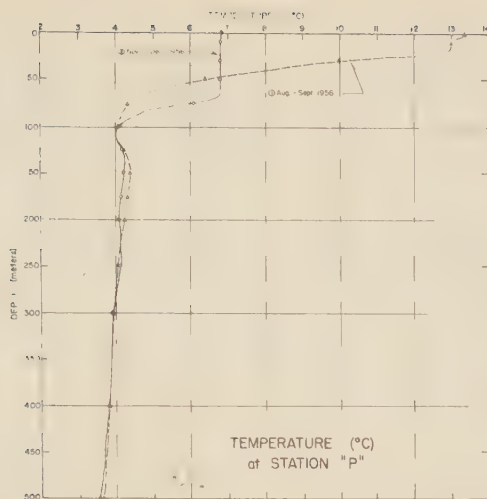


FIG. 26B. Temperature at Station "P", Summer 1956-Summer 1958. Vertical profiles of temperature (0-500 m).

30 m. At a depth of 50 m the annual amplitude is one-half that at the surface. At depths of 75 and 100 m, the annual variations are apparent, but they are even less marked. At a depth of 75 m, there is some indication of semi-annual variations. These have been reported in other parts of the north Pacific Ocean (Robinson, 1957).

A comparison of the annual cycles of air temperature (Fig. 25) and sea temperature between the surface and 100 m depth (Fig. 26A, *middle*) indicates that while the cycle of the surface sea temperature is in phase with that of the air temperature, the cycles of sea temperature below the depth of 30 m are not. In fact, the annual maximum of the sea temperature occurs progressively later with depth. For example, at a depth of 30 m it occurred in early autumn; at 50 m, in late autumn; and at 75 m, in early winter. This phenomenon recurs year after year as Hollister (1956) and Robinson (1957) have already shown.

Appreciable non-seasonal variations of temperature occur in the halocline. At a depth of 150 m for example (Fig. 26A, *bottom*), the temperature varied by about 1 C° during the 2 years. However, there does not seem to be any definite periodicity present in the variations. There was a general increase of temperature during winter 1956 through summer 1958, except during spring to summer, 1957, (Fig. 26A, *bottom*, and Fig. 26B).

In the depths between the top of the halocline (100 m) and the shallow portion of the lower zone (400 m) the variations of temperature are complicated due to the presence of temperature inversion in these levels (Fig. 26A, *top*, *bottom*, and Fig. 26B). These inversions were quite marked and occurred from summer 1956 through spring 1957, but deepened and became imperceptible by summer of 1957 (Fig. 26A, *top*, and Fig. 26B).

Significant variations of temperature occur in the lower zone to a depth of at least 500 m and perhaps to 1000 m (Fig. 26A, *bottom*). The water between the depths of 500 m and 1000 m was about 0.1 C° warmer in 1958 than in 1956 and in the first half-year of 1957.

FACTORS INFLUENCING TEMPERATURE

HEAT TRANSFER ACROSS THE AIR-SEA BOUNDARY

The dominant factor influencing the temperature in the upper zone, and to some extent in the halocline, is heat transfer at the air-sea boundary. The flux of heat through the air-sea boundary is due to the combined effects of incident solar radiation, reflected solar radiation, effective back radiation, evaporation (and condensation), and conduction of sensible heat. The heat transfer equation across the air-sea boundary during a time interval Δt is written:

$$Q_t = Q_i - Q_r - Q_b - Q_e - Q_h \quad \dots (3)$$

where: Q_t is the net heat transfer across the air-sea boundary,

Q_i is the short-wave radiation from the sun and sky, both direct and diffuse,

Q_r is the reflected short-wave radiation from the sea,

Q_b is the effective back radiation (long wave radiation from the sea surface minus that from the atmosphere),

Q_e is the heat transfer by evaporation (and condensation), and

Q_h is the conduction of sensible heat between the atmosphere and the sea.

In this paper, all these quantities are expressed in units of gram-calories per square centimetre per day (g-cal/cm²/day).

The concepts and theories of these components of the heat transfer process are discussed briefly in "The Oceans" (Sverdrup *et al.*, 1942) and in more detail in a report by Anderson (1952). A fairly extensive study of these components has recently been made for a near-shore situation at Triple Island in northern British Columbia (Tabata, 1958).^{*} Here it was found that the annual cycle of incident solar radiation, and the cycle of the combination of evaporation and conduction, controlled the seasonal fluctuations of the net heat transfer across the air-sea boundary. Although the heat loss by effective back radiation was appreciable, the absence of large seasonal variations prevented it from being influential in contributing to the seasonal fluctuations of net heat transfer. A somewhat analogous study is made at Station "P" in the mid-ocean.

The magnitudes of solar radiation for cloudless days are based on values for the coast of British Columbia at Lat. 50°N, interpolated from monthly charts prepared by Mateer (1955). The formula:

$$Q_i = Q_0 (1 - 0.071C) \quad \dots \dots (4)$$

where: Q_i is the solar radiation reaching the sea surface after the effect of cloud has been taken into consideration,

Q_0 is the total incoming solar radiation under clear sky, and

C is the amount of clouds in scale 0 to 10,

is used to correct for absorption of solar radiation by clouds (Sverdrup *et al.*, 1942).

The values of reflection of solar radiation (Q_r) from the sea surface were obtained from charts prepared by Anderson (1952).

The formula:

$$Q_b = 1.141 \{ \theta_s^4 - \theta_a^4 (a + b e_a) \} 10^{-7} \quad \dots \dots (5)$$

where: θ_s is the absolute temperature of the sea surface,

θ_a is the absolute temperature of the air above the sea surface, and

e_a is the vapour pressure (millibars) of the atmosphere where the air temperature is measured, and the constants a and b are related to both the cloud amount and height and were obtained from charts prepared by Anderson (1952),

is used to compute effective back radiation (Q_b) (Tabata, 1958).

For computing evaporation (E in mm/cm²/day and Q_e in g-cal/cm²/day), these formulae are used:

$$E = 0.105(e_s - e_a)u_a \quad \dots\dots (6a)$$

$$\begin{aligned} Q_e &= LE \\ &= 6.13(e_s - e_a)u_a \quad \dots\dots (6b) \end{aligned}$$

where: e_s is the vapour pressure (mb) of the saturated air at the sea surface,

e_a is the vapour pressure (mb) of the air at a height of 6 m above the sea surface, and

u_a is the wind speed (metres per second) at a height of 6 m above the sea surface⁶,

L is the latent heat of vaporization and is equal to 585 g-cal/g.

These formulae are based on the evaporation formula derived by Sverdrup (1937), with the modification proposed by Marciano and Harbeck (1952).

The conduction of sensible heat (Q_h) is computed from values of evaporation multiplied by the Bowen Ratio (Bowen, 1926). The Bowen Ratio is:

$$\frac{Q_h}{Q_e} = \frac{0.61(T_s - T_a)P}{(e_s - e_a)1013} \quad \dots\dots (7)$$

where: T_s is the surface sea temperature (°C),

T_a is the air temperature (°C), and

P is the sea level barometric pressure (mb). (For all practical purposes,

P may be considered as having standard pressure of 1013 mb.)

The data resulting from the computations are shown in Fig. 27. As mentioned in an earlier paper (Tabata, 1958) the accuracy obtainable depends on validity of theories. Lacking direct measurements, the evaluation of such errors are difficult. Errors as large as 20% cannot be considered unreasonable.

As is common in other localities, there is a marked annual cycle of solar radiation. But the magnitude of the absorbed solar radiation (Q_s) is reduced to almost one-third of that which is potentially available (Fig. 27a) because of cloud cover. The annual amplitude of effective back radiation (Q_b) is small compared to that of solar radiation (compare Fig. 27a with Fig. 27b). However, the amount of the heat lost by this process is appreciable. The annual cycle of heat loss by evaporation (Q_e) is marked, with the maximum occurring in winter and the minimum in summer (Fig. 27c). The annual cycle of conduction of sensible heat (Q_h) from the sea to air is generally in phase with that of evaporation but the magnitudes involved are smaller (compare Fig. 27c with Fig. 27d). The main feature of the annual cycle of the net heat transfer (Q_l) across the air-

⁶While air temperatures were observed at a height of about 6 m above the sea surface, wind velocities were observed at a height of about 20 m. Wind speeds at a height of 20 m have been reduced to those at a height of 6 m by subtracting 1.8 m/sec from the observed wind speeds at that height according to data reported by Wagner (1958). This constant reduction of wind speeds may not be correct in detail for various strengths of winds and various stability conditions of air above the sea, but they are assumed to be approximately correct.

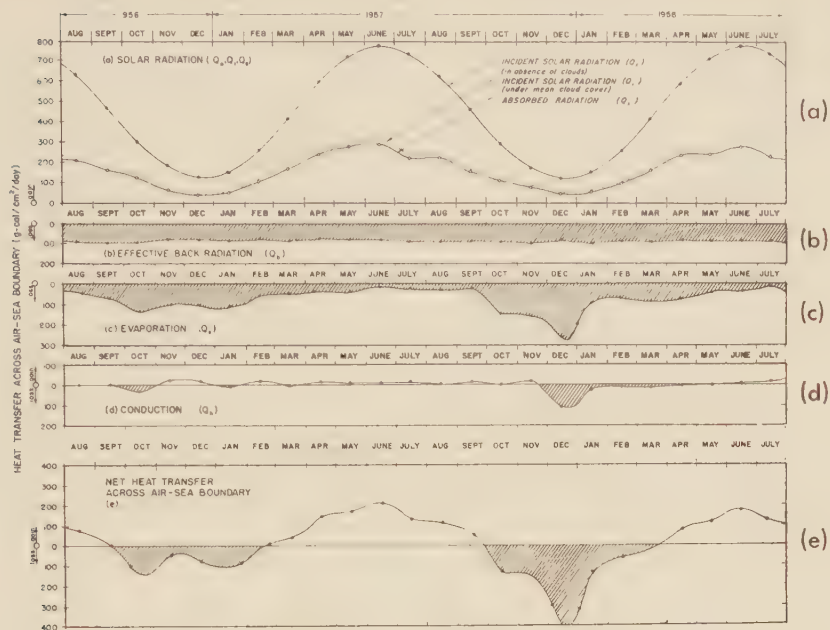


FIG. 27. Monthly mean values of heat transfer process at Station "P", Summer 1956–Summer 1958. (a) Solar radiation (Q_o , Q_i , Q_s). (b) Effective back radiation (Q_b). (c) Evaporation (Q_e). (d) Conduction of sensible heat (Q_h). (e) Net heat transfer across air–sea boundary (Q_t).

sea boundary is that the greatest heat gain occurs in summer (200 g-cal/cm²/day) and the greatest loss (400 g-cal/cm²/day) in winter. The transitional periods during which there is no net heat transfer occur in early spring and in early autumn (Fig. 27e).

During the summer, the main factor contributing to heat gain by the sea is solar radiation. The large loss of heat in winter is attributed mainly to the increase of evaporation and conduction, the former being dominant. Thus the annual cycle of net heat transfer is dependent primarily on these three components of the process. Similar conclusions were reached for heat transfer in the coastal waters (Tabata, 1958).

The sea warms or cools depending on whether or not the net heat transfer is directed into or out of the sea. The rate of change of heat content in a column of water of unit cross sectional area and z cm deep may be calculated as:

$$Q_\theta = \frac{\partial}{\partial t} \int_0^z \rho c_p T dz$$

$$\approx \frac{\overline{\rho c_p} \int_0^z \Delta T dz}{\Delta t} \quad \dots \dots (8)$$

where: Q_θ is the change of heat content (g-cal/cm²/day),

ρ is the density of sea water (g/cm³),

c_p is the specific heat of sea water (g-cal/g/°C) obtained from recent determinations by Cox and Smith (1959),

z is the depth (cm) of the column of water, above which major changes of heat content occur,

$\bar{\rho}$ is the mean density of sea water (g/cm³),

$\bar{c}_p$ is the mean specific heat of sea water (g-cal/g/°C),

Δt is the time interval in days, and

$\Delta T dz$ is the element of area bounded by two temperature-depth curves.

The mean density of sea water in the water column at Station "P" is about 1.0265 g/cm³ and its specific heat 0.954 g-cal/g/°C. Thus the above Formula (8) becomes:

$$Q_\theta = \frac{0.980 \int_0^z \Delta T dz}{\Delta t} \quad \dots (9)$$

From the consideration of net heat transfer at the air-sea boundary at Station "P", the surface water should begin to cool in September, since from this time on, the sea begins to lose heat to the atmosphere, principally from the increase in evaporation. Warming of surface water should commence in March, as from this time on, the sea begins to gain heat, principally from solar radiation (Fig. 27). These two periods, when the net heat transfer changes from being afferent to efferent and vice versa, are confirmed in the annual cycle of surface sea temperatures as shown in Fig. 28. Therefore, the seasonal variations of temperature of the surface water are mainly due to the seasonal variations of net heat transfer at the air-sea boundary.

In order to show the relation between the seasonal variations of net heat transfer and the variations of sea temperature in more detail, the changes of heat content estimated by the heat transfer formulae (Fig. 27e) and the observed changes of heat (Formula (9)) are shown in Table III. It is evident, from the comparison of values shown in that Table, that in most cases more than 50% of the changes of heat content in the upper zone can be attributed to heat transfer, and that most of the seasonal changes of heat content are confined to the upper zone. But during summer through autumn, 1956, only 30% of the change could be accounted for by heat transfer. Evidently, during this period some other process was more influential in changing the temperature.

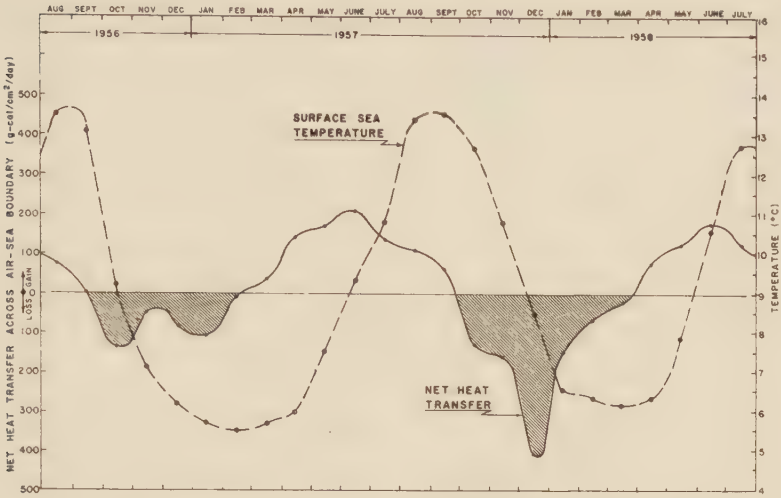


FIG. 28. Relation between surface sea temperature and net heat transfer at Station "P".

TABLE III. Observed seasonal change of heat content in upper zone (0-100 m) and halocline (100-200 m) and changes brought about by heat transfer at air-sea boundary.

Seasons:	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Cruise No.:	56-1	56-2	57-1	57-2	57-3	57-4	57-5	58-1	58-2
Increase (+) or decrease (-) of heat content:									
Upper zone (0-100 m)	-	-	+	+	+	-	-	+	
Halocline (100-200 m)	-	0	+	-	+	+	+	+	
Lower zone (> 200 m)	-	+	negli- gible	negli- gible	negli- gible	+	negli- gible	-	
Observed change of heat content (g-cal/cm²/day) (mainly in upper zone):									
	-197	-79	+126	+194	+138		-473	-130	+198
Depth interval:	0-120	0-130	0-150	0-150	0-100	0-100	0-110	0-130	
Change of heat content (g-cal/cm²/day) from heat transfer at air-sea boundary:									
	-74	-80	+87	+170	+69		-309	-111	+109
Percent of change accounted for by heat transfer at air-sea boundary:									
	32	101	69	88	50	65	85	55	

HORIZONTAL TRANSPORT

The water lying to the south is generally warmer, and that lying to the west and northwest generally colder, than the water at Station "P" (Fig. 11, 12, 13). Hence any current that flows from the south would transport warm water, and any current from the west or northwest would transport cold water into the vicinity.

A transport of relatively warm water from the south, and perhaps south-west, appeared to have caused an additional increase of temperature at the station during summer through autumn 1957 and spring through summer, 1958. During these two periods, heat transfer at the air-sea boundary accounted for only 50% of the increase in temperature.

During the summer of 1957, a temperature increase at the rate of $0.40^{\circ}\text{C}/\text{month}$ occurred. Heat transfer at the air-sea boundary accounted for 50% ($0.20^{\circ}\text{C}/\text{month}$) of the observed increase. From the consideration of horizontal temperature gradients (Fig. 13, *upper*) and surface currents (Fig. 17) for August 1957, and by the use of Formula (2), it is estimated that in the upper zone a temperature increase at the rate of $0.23^{\circ}\text{C}/\text{month}$ could occur. Therefore, the combined effect of heat transfer at the air-sea boundary and advection accounts for the right observed increase. It is probable that the large temperature increase during spring through summer, 1958, and to a lesser degree during winter through spring, 1957, was also due to horizontal transport. This transport is consistent with that causing the change of salinity during the corresponding periods and is attributed to the intrusion of southern water, as mentioned earlier.

The increase of temperature in the halocline from summer 1957 through summer 1958 (Fig. 26A, *bottom*) is also attributed to the transport of warm water from the south (Fig. 13, *lower*). However, a decrease occurred in the halocline during spring through summer, 1957 (Fig. 26A, *bottom*, and third panel of Fig. 26B). A decrease also occurred both above (75 m) and below the halocline (200–300 m) during the same period. The decrease that occurred just below the halocline may be explained by assuming a transport of colder water from the southwest (*lower right* panels of Fig. 12 and 13). Attention is drawn to the positions of the 4°C isotherms for February 1957 (Fig. 12, *lower right*) and for August 1957 (Fig. 13, *lower right*) which indicate that the colder water had, by August 1957, moved to the northeast. It is further evident, from the temporal distribution of the isotherms as shown in Fig. 26A, *top*, that a noticeable movement of the water occurred between spring and summer 1957. However, the temperature decrease in and just above the halocline must have been due to the transport of cold water from the northwest which was the only source of cold water at these depths (*lower left* panels of Fig. 12 and 13).

The manner in which the intrusion of warm water affected the water at Station "P" may also be illustrated by comparing the T-S characteristics of the water at various periods, as shown in Fig. 29. Attention is drawn to the curves for 1957 and 1958. The gradual shift of the T-S characteristics, corresponding to the progressive increase of temperature and salinity above the lower zone, is quite evident. Comparison of these with the T-S classification of water masses in the region (Fig. 30—Tully and Dodimead, 1957) indicates that the water at the station has undergone a gradual change towards a more southern type. A comparison with the water lying south of the Subarctic Boundary (Fig. 7) suggests that the intruding water had characteristics intermediate between the Subarctic and Subtropic Waters.

A transport of relatively cold water from the northwest during summer through autumn, 1956, and autumn through winter, 1957, appears to have caused

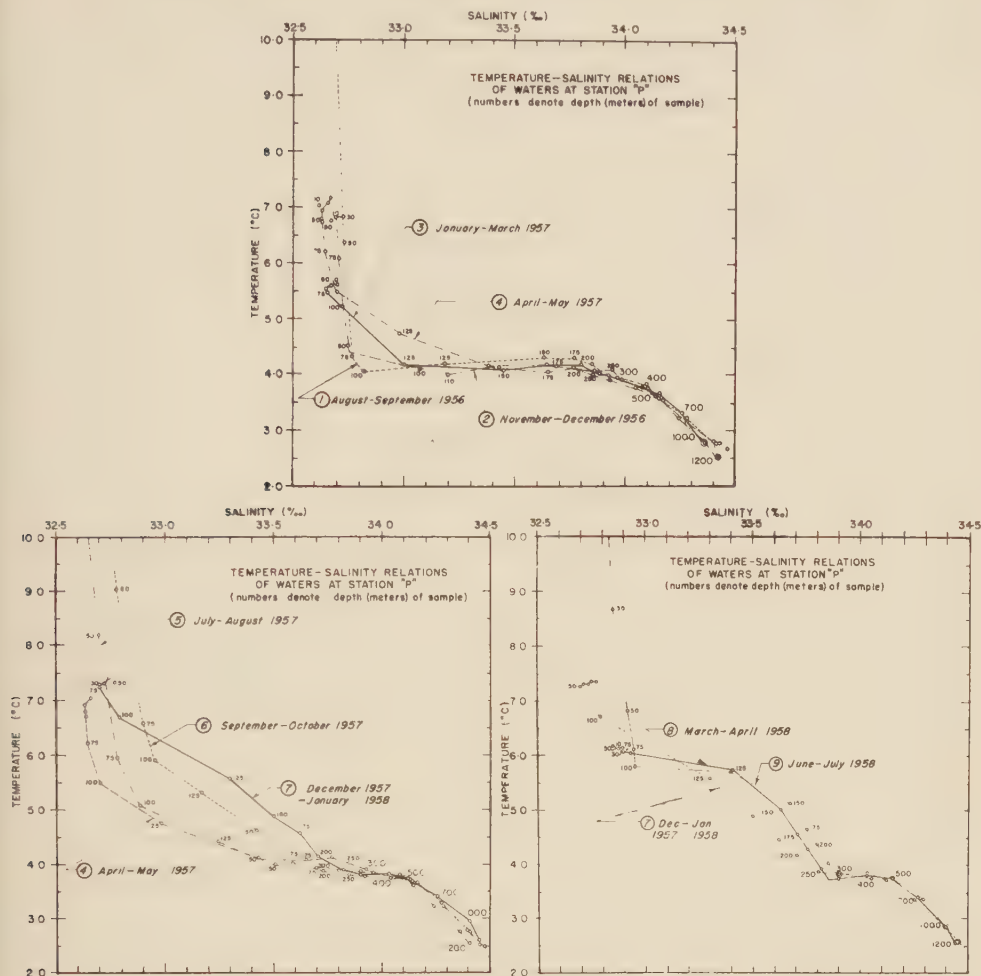


FIG. 29. Temperature-salinity relations of water at Station "P", Summer 1956-Summer 1958.

a decrease of temperature, as in both cases heat transfer at the air-sea boundary could account for only a portion of the decrease (Table III).

During summer 1956, the isotherms in the vicinity of Station "P" lay almost parallel to the direction of the surface geostrophic current (Fig. 11, *upper*, and Fig. 17). Thus the transport of water due to this current could not alter the temperature at the station. However, a transport of colder water from the west or northwest could cause a decrease. This seems likely, as during summer 1956 colder water lay in these directions (Fig. 11, *upper*). Also, during October 1956 the winds were generally from these directions (Fig. 20d and 21, *lower*). If the distribution of surface temperature observed in summer (Fig. 11, *upper*) can be assumed to have continued through the autumn, then it may be concluded that the transport of cold water associated with these winds were the main

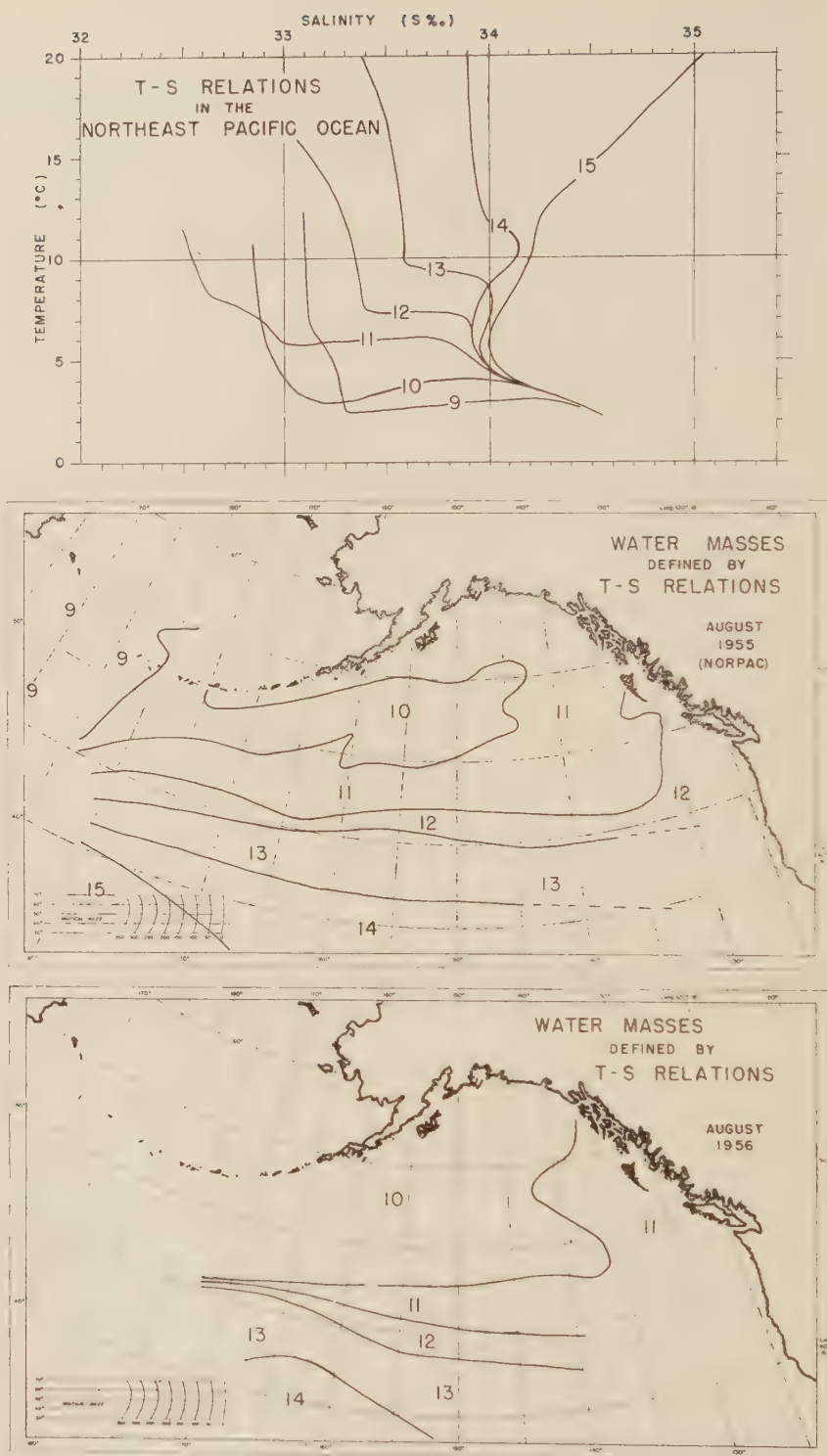


FIG. 30. Temperature-salinity classification of water masses of northeast Pacific Ocean region (Tully and Dodimead, 1957).

cause for the decrease of temperature that occurred between summer and autumn of 1956. The corresponding increase of salinity in the halocline (Fig. 18B) lends support to the concept of transport from these directions.

There is one temperature feature in the halocline (100–200 m depth) for summer and autumn, 1956 (Fig. 11, *lower*, and first panel of Fig. 26B), that is of particular interest. During the summer, Station "P" appeared to lie in the axis of a tongue of cold water which originated in the "dome" area. The tongue, characterized by the 4°C isotherm (Fig. 11, *lower*) continued past the station until it finally lost its identity about 200 miles to the southeast. From consideration of the vertical temperature gradients (first panel of Fig. 26B) it is reasonable to anticipate a progressive increase of temperature in the minimum temperature layer, due to eddy diffusion of heat. But the temperatures of this layer in summer and in autumn were exactly the same. It is speculated that the rate of horizontal movement of this tongue, presumably to southeastward, was just sufficient to neutralize the increase of temperature that may have resulted from vertical eddy diffusion of heat.

Only 65% of the decrease of temperature (Table III) during autumn through winter, 1957, is due to heat transfer at the air-sea boundary. The remainder is attributed to wind transport of colder water from the west and northwest since winds were generally from these directions in December 1957. This is consistent with the explanation given earlier for the change of salinity at the station during the same period.

VERTICAL MIXING

As shown earlier, the homogeneous layer thickened progressively from autumn through winter due to vertical mixing (Fig. 22). This process brings about the redistribution of heat, as well as salt, in the homogeneous layer. By doing so, it transports the warmer water downward and the colder water upward (Fig. 23, *right*). The net result is that warming of water at some depths in the upper zone may occur, even when the sea is actually losing heat to the atmosphere. It is this mixing that causes the maximum annual temperature to occur progressively later with depth, in the upper zone (Fig. 26A, *middle*).

OTHER FACTORS

It is possible that both lateral and vertical eddy diffusion of heat could also affect the temperature of the water at Station "P". It is assumed that their effects are small compared to those of heat transfer at the air-sea boundary and horizontal transport.

However in summer 1957, lateral eddy diffusion may have had some effect. As shown in Fig. 13, *upper*, the water at the station was almost surrounded by warmer water. And although it is difficult to prove, it is possible that a temperature increase at the station may have resulted from lateral eddy diffusion.

VARIATIONS OF DISSOLVED OXYGEN CONTENT

The dissolved oxygen, together with the oxygen solubility and the degree of saturation, of the surface water at Station "P" are shown in Fig. 31 (*upper part*). In Fig. 32 are shown the oxygen in the surface and subsurface waters. It is evident from the comparison of the annual cycle of the oxygen, and of the solubility

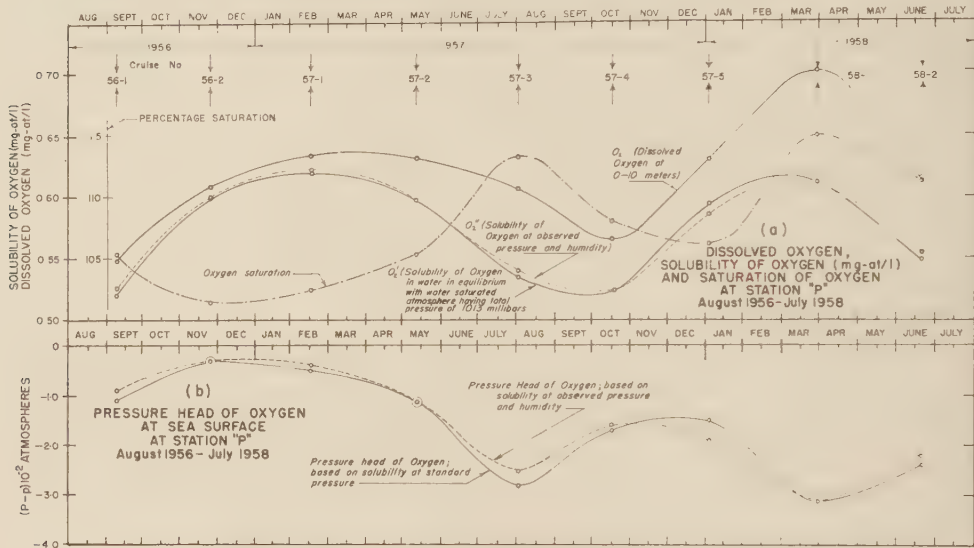


FIG. 31. *Upper part*—Seasonal values of dissolved oxygen content, solubility of oxygen in water, and degree of saturation, of the surface water at Station "P", Summer 1956–Summer 1958. *Lower part*—Pressure head of oxygen at the sea surface at Station "P", Summer 1956–Summer 1958. (The data over the approximate 6-week period are combined and plotted as a single point. This corresponds to observations at mid-date of the cruise period.)

(Fig. 31 (*upper part*) and middle panel of Fig. 32A), that marked annual variations of oxygen which are in general phase agreement with those of solubility occur at the surface and to a depth of 30 m. The oxygen in the surface water reaches a maximum in early spring and a minimum in early autumn. The surface water remains supersaturated throughout the year. It reached maximum supersaturation in summer 1957, and again in spring 1958, and minimum in the two winters.

Appreciable annual variations of oxygen occur at depths of 50 and 75 m (Fig. 32 A and B) and they appear almost in phase with those at the surface. However, in some periods, as during autumn through winter 1956, they were in opposite phase to those at the surface.

The oxygen in the depths above 75 m decreases from spring through autumn (Fig. 32 A and B). But it does not seem to decrease at the same rate at all depths. In fact, the rate decreases with depth, being largest at the surface, and becomes progressively smaller with depth. Because of this decrease and

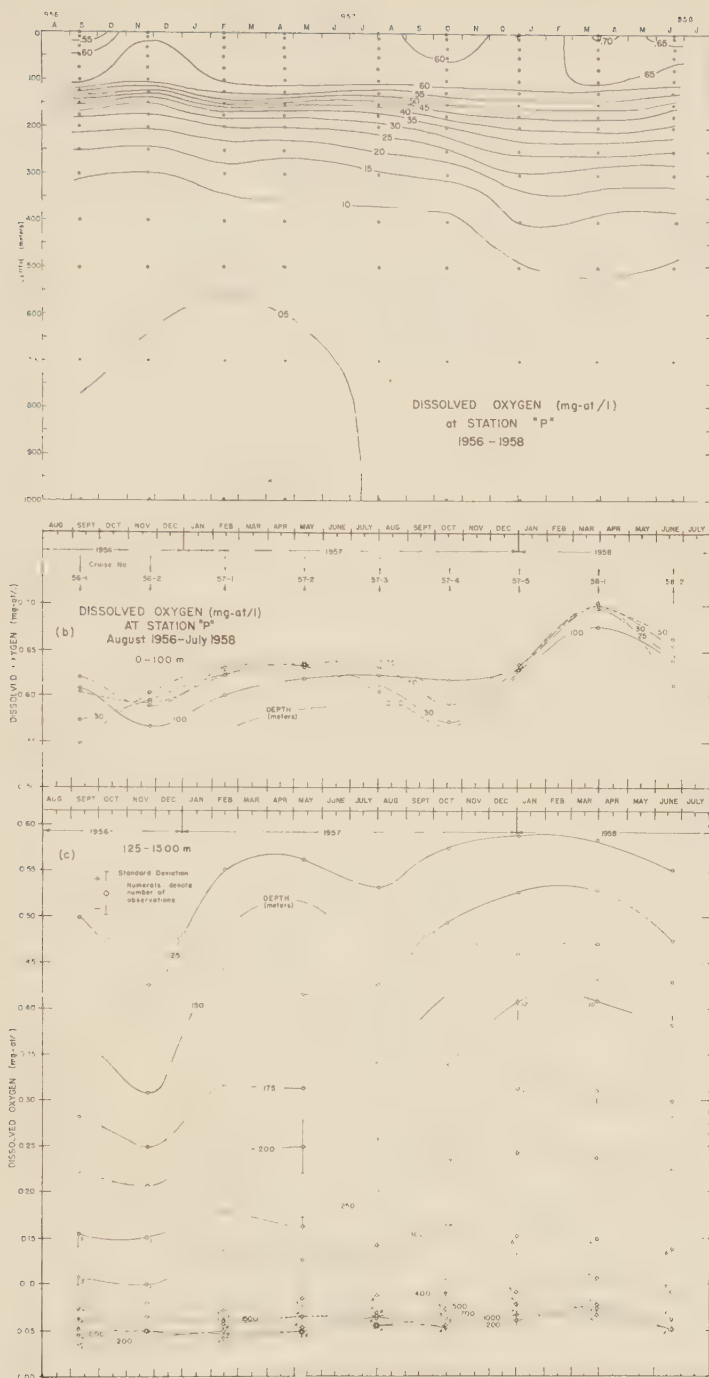


FIG. 32A. Dissolved oxygen content at Station "P", Summer 1956–Summer 1958. (The data over the approximate 6-week period are combined and plotted as a single point. This corresponds to observations at mid-dates of the cruise period.) *Top*—Seasonal distribution of dissolved oxygen content (0–1000 m). *Middle*—Seasonal values of dissolved oxygen content at depths: 0, 10, 30, 50, 75, and 100 m. *Bottom*—Seasonal values of dissolved oxygen content at depths: 125, 150, 175, 200, 300, 400, 500, 700, 1000, 1200, and 1500 m.

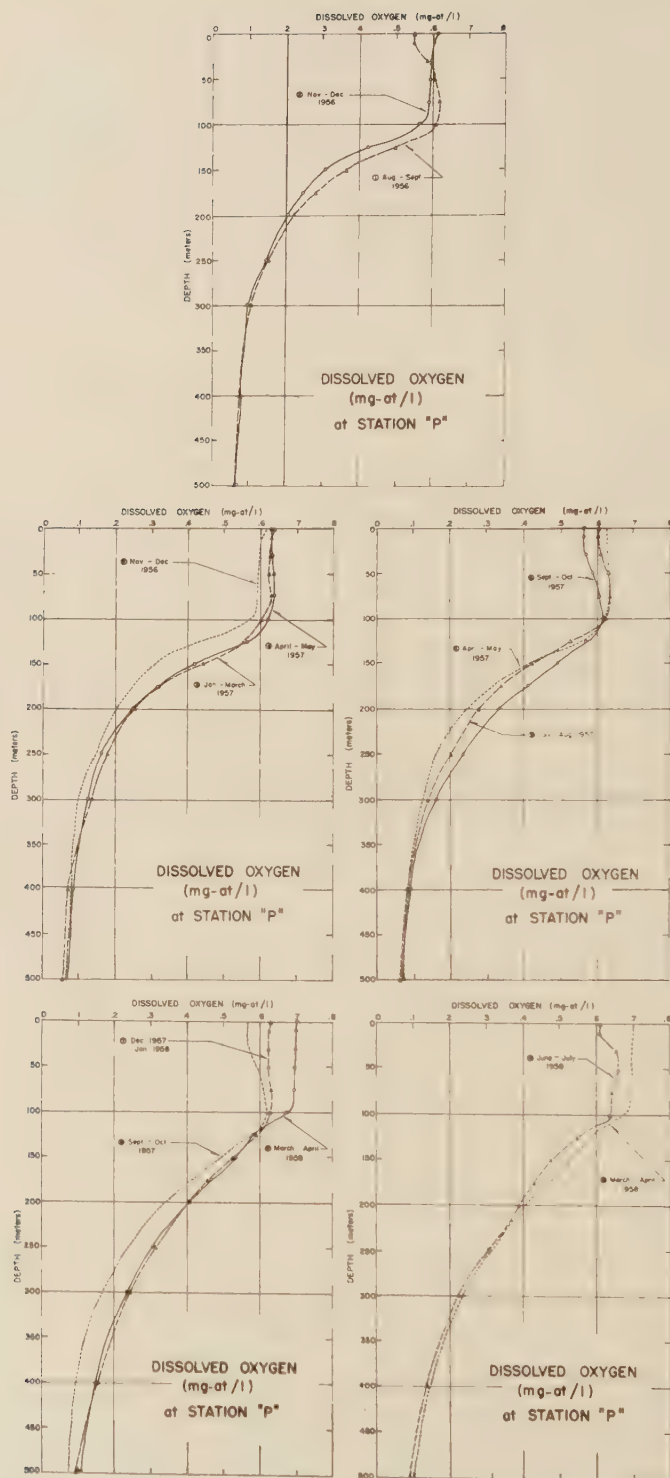


FIG. 32B. Dissolved oxygen content at Station "P", Summer 1956-Summer 1958. Vertical profiles of dissolved oxygen content (0-500 m).

because the oxygen decreases with depth from 100 m downward, it follows that in the summer and early autumn a maximum oxygen layer occurs between 50 and 100 m depth.

There is little evidence of definite annual variations of the oxygen at the depths below 100 m. However, there are conspicuous non-annual variations in both the halocline and the lower zone. For instance, at depths between 150 and 500 m, the oxygen doubled from autumn 1956 to spring 1958 (Fig. 31, lower part). The trend in the lower zone at depths between 400 and 1000 m was generally similar to that in the halocline. The minimum occurred in winter 1956, and the maximum in winter 1957. The variations at 1200 m depth were more irregular however, than at depths less than 1000 m (Fig. 31, lower part).

FACTORS INFLUENCING DISSOLVED OXYGEN CONTENT

OXYGEN EXCHANGE AT THE AIR-SEA BOUNDARY: SOLUBILITY OF OXYGEN IN SEA WATER

Oxygen exchange at the air-sea boundary would occur if there is a difference of partial pressure of oxygen across the sea surface. In areas of large production of oxygen (by photosynthesis) the excess oxygen produced would result in excess partial pressure of oxygen in the sea, hence oxygen would tend to escape to the atmosphere. On the other hand, in areas of high organic consumption, or in areas of upwelling where unsaturated water is brought to the surface, oxygen would tend to be absorbed, because the partial pressure of oxygen in the sea would probably be less than in the atmosphere. The surface water in contact with the atmosphere would tend to reach equilibrium by releasing or absorbing oxygen until the water is saturated. In fact, large areas of the ocean are essentially in equilibrium with the atmosphere (Richards and Corwin, 1956).

The solubility of oxygen in sea water decreases with increasing temperature and salinity. The values of solubility have long been based on the data obtained by Fox (1909). However, Truesdale *et al.*, (1955) obtained values that were generally 4% lower than those obtained by Fox. Recent work by Steen (1958) provides values that are in agreement with those of Fox. Controversy continues regarding the correct values of solubility.

At Station "P" the temperature varies annually by more than 8 C°, and the salinity by 0.05‰. The variation due to the salinity change is less than 2% of that due to the temperature change. Consequently, temperature is the dominant factor controlling the solubility of oxygen at the station.

The values of solubility of oxygen of the water at Station "P" were determined from a nomograph prepared by Richards and Corwin (1956), based on measurements of Truesdale *et al.* Their values were chosen because they seemed to give reasonable values for saturation of the surface waters in the ocean.

The solubility values of Truesdale *et al.* were obtained for equilibrium conditions established under a standard atmosphere (1013 millibars) saturated with water vapour, at the temperature in question. For detailed work, consideration of the atmospheric pressure and humidity of the air is necessary.

Carritt (1954) has pointed out that the seasonal changes in atmospheric pressure that occur over the ocean are sufficient to impart measurable change in the solubility, by as much as 0.03 mg-at/l. Richards and Corwin (1956) have shown that the humidity effect can cause a change of 1% in the saturation values.

The solubility values obtained under standard conditions may be corrected for pressure and humidity effects from the Richards and Corwin formula:

$$\frac{O_2''}{O_2'} = \frac{P - e_s(h/100)}{1013 - e_s} \quad \dots\dots (10)$$

where: O_2'' is the solubility of oxygen (mg-at/l) in water in equilibrium with an atmosphere having a pressure of P (mb) and a relative humidity of $h\%$,

O_2' is the solubility of oxygen (mg-at/l) in water in equilibrium with a water-saturated atmosphere with a standard pressure of 1013 mb (solubility data of Truesdale *et al.*, 1955),

e_s is the vapour pressure (mb) of water at the observed temperature.

In the upper part of Fig. 31 are shown the two sets of values: those under standard conditions (continuous curve), and those under observed atmospheric conditions (dashed curve). Comparison indicates that the differences are small.

Redfield (1948) examined the problem of oxygen exchange at the air-sea boundary in the Gulf of Maine. He evaluated the pressure head of oxygen at the sea surface as:

$$P - p = p \left(\frac{O_2' - O_2}{O_2'} \right) \quad \dots\dots (11)$$

where: P is the partial pressure of oxygen in water-saturated atmosphere and is equal to $0.21(1 - e_s)$, e_s being the vapour pressure of water at the sea surface,

p is the partial pressure of oxygen in sea water (oxygen tension) and is equal to $p \left(\frac{O_2}{O_2'} \right)$,

O_2' has the same meaning as in Formula (10), and

O_2 is the dissolved oxygen content of water.

The positive values of $(P - p)$ indicate that oxygen is directed from the atmosphere to the sea.

From his study, Redfield concluded that during the winter the pressure head was positive, favouring the movement of oxygen from the atmosphere into the sea, and *vice versa* in summer. Richards and Corwin recomputed the values of pressure heads, employing the solubility values of Truesdale *et al.* and concluded that the conditions favouring the escape of oxygen from the sea to atmosphere are more pronounced, and prevailed during a larger part of the year than Redfield has estimated.

Computations of differences of the pressure heads were made for the water at Station "P", and from the results, as shown in the lower part of Fig. 31, it is

evident that the conditions favouring the escape of oxygen from the sea to atmosphere prevail throughout the year, being most pronounced in spring and summer. In winter of 1956-1957 the partial pressures of oxygen in the sea and atmosphere were almost in equilibrium. The continuous curve in the Figure represents values of pressure head difference under standard conditions, and the dashed curve represents values under observed atmospheric conditions. Comparison indicates that an error as large as 20% may be introduced by using standard rather than actual conditions.

The apparent correlation between the oxygen and the solubility in the surface water (upper part of Fig. 31) suggests that the seasonal variations of the oxygen are governed by the seasonal variations of solubility. It can also be seen from the comparison of temperature-depth profiles (Fig. 26B) and the oxygen-depth profiles (Fig. 32A, *bottom*) that the changes of oxygen in the depths between 0 and 75 m are correlated with the changes of temperature at corresponding depths; that is, in and above the thermocline. It follows that the structure of oxygen during the summer, with a maximum occurring at depth of about 75 m, is a consequence of the decrease of solubility above the thermocline.

PRODUCTION AND UTILIZATION OF DISSOLVED OXYGEN BY MARINE ORGANISMS

In the euphotic zone of the ocean, which is controlled by the depth of the penetration of light, oxygen is produced by photosynthesis by the phytoplankton. Oxygen is utilized principally by respiration of the zooplankton and fish (Sverdrup *et al.*, 1942). However, little study, if any, has been made to estimate the production and utilization of oxygen in the waters of the northeast Pacific Ocean.

Large values of supersaturation of the surface water frequently denote extensive photosynthetic activity (Sverdrup *et al.*). The relatively large values observed during summer 1957 and spring 1958 may possibly be due to high production by phytoplankton. Moreover, the fact that the surface water was supersaturated throughout the year suggests that even in winter some production must have taken place.

There is an appreciable population of zooplankton at Station "P", particularly during the summer (McAllister, 1960) and these animals might affect the distribution of oxygen. But there does not appear to be any apparent correlation between the size of zooplankton population and the oxygen in the upper zone. It is likely that the effect of solubility masks changes of oxygen brought about by respiration of these animals.

HORIZONTAL TRANSPORT

As in the case with the discussions of salinity and temperature, horizontal transport of water is likely to influence the oxygen at Station "P". But it appears that changes associated with transport are also masked by the effect of solubility. However, in the halocline and in the lower zone, where the effect of change of solubility is small, there is evidence that horizontal transport is effective in changing the oxygen.

The progressive increase of oxygen in the halocline and in the lower zone during summer 1957 through spring 1958 (Fig. 32A, *middle* and *bottom*) is attributed to the northward transport of the water. As shown in Fig. 14, 15, 16, the oxygen at these levels is greater to the south and less to the north. Hence the "oxygen-deficient" water is removed from the vicinity of the station by transport to the north and is replaced by water of a higher oxygen content from the south. This is consistent with the intrusion of warm, saline water into the region, as discussed earlier.

The decrease that occurred between summer and autumn, 1956, is in all likelihood due to the intrusion of the "oxygen-deficient" water from the northwest (Fig. 14, *lower left*). This is consistent with the argument presented earlier in which such intrusion was inferred from the changes of salinity and temperature.

The decrease that occurred below the depth of 500 m during spring through summer, 1958, suggests that perhaps a retreat southward of the relatively "oxygen-rich" water occurred.

OTHER FACTORS

Redistribution of oxygen by vertical mixing occurs at the same period when the salinity and temperature are affected. The increase of oxygen in the upper 50 m depth that occurred during summer through autumn, 1956 (Fig. 32B, *first panel*), is mainly the result of such mixing.

Lateral eddy diffusion may have tended to decrease the oxygen at Station "P" during summer 1957, when the oxygen at the station was greater than in any of the surrounding area except to the north (Fig. 16, *upper*).

SUMMARY AND CONCLUSIONS

The principal feature of the annual variations of salinity of the water at Station "P" is that they are most marked in the upper zone and in the halocline, and are less marked in the lower zone. Noticeable variations occur at all depths to at least 1000 m. There is little evidence of definite cyclic annual variations in the upper zone, except at a depth of 100 m. During 50% of the time, the trend of variations in the upper zone, halocline, and lower zones is similar.

The annual cycle of surface sea temperature is in phase with that of the air temperature. Moreover the annual amplitude of the variations of surface sea temperature is similar to that of the air temperature. Marked annual variations of temperature occur to depth of 30 m, and to lesser extent to depth of 100 m. Appreciable non-seasonal variations of temperature occur in the halocline and also in the shallow portion of the lower zone. There was a progressive increase of temperature at these levels during spring 1957 through summer 1958. A minimum and a maximum temperature layer occurred during the latter half of 1956 and continued to the spring of the following year but became imperceptible by the summer.

Marked annual variations of dissolved oxygen content occur in the upper zone, especially in the upper 30 m depth, the values reaching maximum in winter

or spring, and dropping to minimum in summer or autumn. The variations of oxygen, and those of solubility of oxygen, in the surface water are similar in both the phase and amplitude. The surface water is supersaturated throughout the year, this condition being more pronounced in summer 1957 and spring 1958 and less so in the winters. There is little evidence of the annual variations below the depth of 100 m. However, in both the halocline and the lower zone appreciable variations with a period greater than one year are evident.

Dilution of water in the upper zone, due to excess precipitation over evaporation, was mainly responsible for the decrease of salinity during summer through winter, 1956. But during winter through spring, and autumn through winter, 1957, only 50% of the decrease could be accounted for by this excess. From spring 1957 through summer 1958, the salinity generally increased (except between autumn and winter, 1957), despite the tendency to decrease from excess precipitation.

The principal factor influencing the temperature in the upper zone is heat transfer at the air-sea boundary. It accounted for more than 80% of the temperature changes during autumn through winter, 1956, spring through summer, 1957, and winter through spring, 1958. It accounted for 50 to 75% of the changes during winter through spring, 1957, summer through winter, 1957, and spring through summer, 1958. During summer through autumn, 1956, it accounted for only 30%.

The close correlation between the oxygen and the solubility of oxygen in the surface water indicates that the variation of the oxygen is determined primarily by the solubility, and hence oxygen exchange across the air-sea boundary. The decrease of oxygen in the upper zone during spring through summer is related to the increase of temperature above the thermocline. The occurrence of maximum-oxygen layer at a depth between 50 and 100 m in summer and autumn is attributed to this effect. Hence the temperature, which affects the solubility, appears to be the dominant factor influencing the oxygen above the thermocline. The persistent supersaturation of the surface water, and the persistent higher values of partial pressure of oxygen in the water, indicate that a condition favouring the escape of oxygen from the sea to atmosphere prevails throughout the year. This was most pronounced in summer 1957 and spring 1958. During such periods when supersaturation was relatively high, it is possible that oxygen may have been produced in large quantity by high photosynthetic activity.

Horizontal transport seems to exercise appreciable influence on the properties of water at Station "P". The general increase of salinity, temperature, and oxygen that occurred during spring 1957 through summer 1958 was due to the northward transport of water into the region. Transport of water from the general vicinity of the "dome" lying northwest of the station appears to have caused an increase of salinity, decrease of temperature, and decrease of oxygen in the halocline and lower zone during summer through autumn, 1956. The large decrease of temperature in the upper zone during this period was due mainly to this transport. The occurrence of winds from the west and northwest during this period, leads one to suspect that the transport in the upper zone may

be due to winds. The large decrease of salinity in the upper zone during autumn through winter, 1957, was also partly due to such winds.

Vertical mixing causes the homogeneous layer to thicken during autumn through winter. This mixing results in the redistribution of properties of water in the vertical column. The increase of salinity in the shallow portion of the upper zone, and the decrease in the deeper portion in winter, are attributed to this effect. It also accounts for the occurrence of an annual salinity minimum at a depth of 100 m in winter. The progressive lag with depth at which the maximum annual temperature is reached is also due to this effect. This also contributes partly to the increase of oxygen in the upper 50 m depth during the late autumn.

Effects of lateral and vertical eddy diffusion have not been treated quantitatively owing to the uncertainty in the values of eddy coefficients. However, lateral eddy diffusion may affect the properties of water at the station especially when it is surrounded with water having different properties.

ACKNOWLEDGMENTS

Grateful acknowledgment is made to Captain J. A. Sleight and the officers and men of C.M.S. *St. Catharines* who ably assisted in the observations; to the Director of the Meteorological Services of the Canada Department of Transport for providing the meteorological data; to the Extended Forecast Section of the United States Weather Bureau for making available the monthly mean sea level pressure charts; and to the staff of this Board's Pacific Oceanographic Group, especially Mr C. D. McAllister, who made observations and assisted in the processing of the data and particularly to Dr N. P. Fofonoff and Dr J. P. Tully for their interest, suggestions, and criticisms in the work. Acknowledgment is also made to Mrs M. Robinson of Scripps Institution of Oceanography and Mr J. F. T. Saur, Jr. of the United States Fish and Wildlife Service, who made critical reviews of the paper.

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Order of Succession of Different Types of Infraoral Lamina in Landlocked Sea Lamprey (*Petromyzon marinus*)¹

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ABSTRACT

Infraoral lamina were studied of 630 lampreys from Lake Erie, Ontario, Lake Seneca, New York, and the Pèrè Marquette River, Michigan. The number of cusps on the first set of the lamina is always repeated in consecutive new sets, but the size of the cusps and their orientation vary. The width of the lamina increases slowly from 4.5 to 16.5 mm, with successive replacements of the corneous sheath. The main types of lamina are: *normal* (teeth large, evenly spaced, their points nearly parallel), *inclined* (teeth large, evenly spaced, their tips inclined mesad), and *rosebud* (teeth very small and clustered near the middle of the lamina; concentric lines on the basal portion). There is also the type *intermediate* between inclined and normal. Newly transformed lampreys and others less than 180 mm long have normal laminae. The rosebud lamina is characteristic of half-grown specimens, being most frequent among lampreys 250–400 mm long. In adults, feeding in lakes, the predominant type is the inclined lamina. In spawning specimens the normal lamina is most characteristic. Thus the usual succession throughout life is: normal, rosebud, inclined, and finally normal again. In spawning specimens there are two new sheaths underneath the old one, one below the other.

INTRODUCTION

WHILE EXAMINING the “tongue” (lingual lamina) in several hundreds of spawning sea lampreys from the St. Lawrence River, Great Lakes, and Finger Lakes of New York, the senior author observed closely the peculiarities in the development of other teeth. Lampreys from these different localities exhibited close similarity in the type of the cusps on the infraoral lamina. Typically their cusps were strong, sharp, and parallel to each other. Then two years ago, Mr W. J. Christie kindly sent us some half-grown *Petromyzon marinus* from the Bay of Quinte, Lake Ontario. Several of them exhibited a rather unusual type of infraoral lamina, which we called “rosebud” (Table II, Fig. 1, 3). Later we secured more half-grown specimens of sea lamprey from other localities, such as Lake Erie, Lake Seneca and the Pèrè Marquette River, in some of which the “rosebud” type of infraoral lamina was present also.

To find out why some specimens have normally developed infraoral laminae, while others have the “rosebud” type, the present investigation was undertaken. Altogether, 630 transformed specimens of landlocked sea lampreys from five different localities have been studied in detail (Table I).

¹Received for publication May 15, 1961.

The material from Lake Erie consisted of newly-transformed, half-grown and adult lampreys, all of which were feeding. A sample from Big Creek, a main spawning stream in Lake Erie, was composed of lampreys which would have spawned in 2 or 3 weeks. From the Lake Seneca area we had a sample of immature specimens feeding in the lake, and a sample of spawning lampreys caught in Catherine Creek. Lampreys from the Père Marquette River represented an early spawning run; they would have spawned in about 3 or 4 weeks.

METHODS OF MEASUREMENTS

Measurements listed below were made with dividers on the left side of the specimen and expressed in millimetres.

Length of the lamprey: The total length, measured from the anterior-most tip of the oral fimbriae to the end of the caudal fin.

Branchial region: From the front of the first gill opening to the posterior edge of the last (7th) gill opening.

Distance between dorsal fins: This distance was measured along the horizontal line of the back, from the hind end of the first dorsal fin base to the origin of the second dorsal fin. The origin of the second dorsal fin was considered the anterior point where the profile of this fin starts to rise from the horizontal line. In young and half-grown specimens the distance between the two dorsal fins is very distinct. In mature specimens this distance diminishes greatly and sometimes, in spawning lampreys, both fins can touch each other. Also in spawning specimens, the skin along the back swells considerably and thus obstructs from view the true origin of the second dorsal fin. For this reason the measurements of the distance between the two dorsal fins in younger specimens is more accurate than in spawning ones. Nevertheless, the difference in the distance between two dorsal fins of lampreys of different ages is very pronounced and amply compensates for the occasional inaccuracy of this measurement. The distance between the two dorsal fins in spawning specimens usually varies from 12 to 30%, average 22% of the length of the branchial region; in young or half-grown lampreys this distance varies from 40 to 70%.

Width of intestine: The exterior diameter of the intestine, empty or with food, was measured immediately behind the hind end of the liver. In spawning specimens the width varies from 1.5 to 3 mm, while in half-grown specimens, actively feeding, it may be as much as 27 mm.

Infraoral lamina: Maximum width of the infraoral lamina was measured, with fine dividers, along the anterior surface of its base between the two most distant points. In young specimens these measurements were made under a binocular microscope. By the same method the distances along the anterior surface between the exterior bases of the extreme cusps was measured; this is called a "cusp-row" in this paper. In Table II this distance is expressed as a percentage of the maximum width of the lamina.

COLOUR PHOTOGRAPHS

Due to the smallness of lamprey teeth and their yellow or orange colour, it is not easy to show their exact shape in black-and-white photographs. Hence colour photographs were taken, some of which are reproduced in Fig. 4. After several trials, the following procedures were adopted. We employed the Linhof Super Technica camera, with triple extension and 60 or 90 mm lenses. The construction of this camera permits the final critical focusing to be made on the ground glass of the swinging back, and hence avoids a distortion in the shape of the infraoral lamina cusps. The camera was fixed on a solid tripod. As a source of illumination several 6-volt spotlights were used. We used 4×5 inch cut films for 3200° K light. The exposure time varied from 1 to 10 seconds at *f*16-32.

The discs of lampreys were photographed while submerged in water and held in position by pins stuck to a cork sheet. The corneous sheaths and the infraoral laminae with their cartilaginous bases were photographed in dry condition. To hold them in a proper position, they were embedded into modelling clay ("plasticine") of different colours. The empty corneous sheaths retained the normal position very well; however the cartilaginous bases of the laminae, owing to desiccation, were bent inward and thus somewhat distorted the natural shape of the infraoral laminae.

The series of old and new sets of the infraoral lamina from any one lamprey were embedded into a putty of a particular colour, thus helping to identify the individuals. The infraoral laminae and their corneous sheaths were photographed from the front, that is, the anterior surface.

STAGES OF MATURITY

To determine accurately the stages of maturity in lampreys, histological slides should be made and sex cells properly measured. However, for the purpose of the present paper, only general characteristics, applicable to both sexes, are required.

For a convenient comparison of the degrees of gonad development we use a numerical system, based not only on the degree of development of the sex cells, but also on the degree of degeneration of the intestinal tract and on the decrease of the space between the two dorsal fins at the onset of sexual ripening caused by shrinkage in the body length (Vladykov and Follett, 1958).

STAGE 0: IMMATURE CONDITION. At least $\times 60$ magnification required to distinguish sex cells, gonads like narrow cords; intestine functional; dorsal fins widely separated, the distance between them averaging 50% of the branchial region; lampreys usually smaller than 250 mm in length.

STAGES 1 AND 2: EARLY DEVELOPMENT OF GONADS. Sex cells distinguishable at lower magnification; although gonads are a little larger in Stage 2 than in Stage 1 they are very narrow; lampreys feed greedily and their intestine is very large, up to 27 mm in external diameter; dorsal fins widely separated, distance between them varies from 40 to 70% of the branchial region; size typically larger than 250 mm.

STAGE 3: MID-POINT OF DEVELOPMENT OF GONADS. Gonads of each sex can often be distinguished with the naked eye by their characteristic appearance, and they occupy more than half of the body cavity; colour of the liver in this and preceding stages is yellow; intestine still large but beginning to diminish in diameter (Table XII); distance between dorsal fins as wide as in the preceding stages. Lampreys reach their maximum size.

STAGE 4: PRE-SPAWNING. Gonads are easily distinguishable by the naked eye and occupy nearly the whole of the body cavity; intestine no longer functional, and greatly reduced, its diameter less than 6 mm (Table XII); space between dorsal fins has begun to decrease, this distance averaging about 40% of the branchial region; in males a "rope-like" ridge along the back begins to appear; colour of liver greenish rather than yellow.

STAGE 5: SPAWNING. Gonads occupy entire body cavity; intestine at its maximum degeneration, its diameter 3 mm or less (Table XII); liver green; pronounced shrinkage in body length, the distance between the dorsal fins 12 to 30% of the branchial region; an "anal fin-like fold" present in females and a "rope-like" ridge along the back in males.

STAGE 6: POST-SPAWNING. Body cavity practically empty of sex cells; general appearance similar to Stage 5; specimens dying.

Lampreys in Stages 0 to 2 live in lakes and can be called *immature* specimens. Lampreys in Stage 3 are *adults of the early spawning run* (Tables VIII, XV), as they approach their respective spawning streams early in spring. Lampreys in Stages 4–6, can be called *mature* specimens; they are present in spawning streams.

Several authors who have studied *Petromyzon marinus* have observed a pronounced shrinkage of the body in spawning specimens. Lennon (1954, p. 275) reported a shrinkage in length from 1 to 3 inches in Lake Huron lampreys. Wigley (1959, p. 593) observed in Cayuga Lake that spawning lampreys lose 11% of their length in males and 18% in females. Cotronei (1926) found even greater shrinkage in anadromous specimens of sea lamprey from Italy, up to 20%.

INFRAORAL LAMINA

On the sucking disc of the lamprey, among the numerous yellow or orange corneous teeth the infraoral lamina is the largest structure (Fig. 1). It is arch-like in shape, with a convex anterior surface, and bears several strong cusps on its upper edge. Very little attention has been given to this lamina in papers dealing with *Petromyzon marinus*.

The number of cusps on the infraoral lamina varies from 6 to 10 both in anadromous specimens (Vladykov, 1949, p. 22) and in landlocked specimens from Lakes Cayuga and Seneca in New York (Wigley, 1959, p. 574). During the present study we found a single male, 419 mm long, from Père Marquette River with only 5 cusps on the infraoral lamina.

In the sea lamprey, as in other parasitic species, there is a periodic replacement of all old teeth by new ones. Bridge (1932, pp. 247–248), quoting Warren (1902, p. 632), stated that in lampreys "each tooth consists of an axial papilla of the dermis, sometimes enclosing a pulp-cavity, and invested by the epidermis, and also by a stratified horny cone which forms the projecting hard part of tooth. . . The old teeth are vertically replaced by new teeth developed beneath the functional teeth".

Similar periodic changes are observed in the infraoral lamina as well. It is unfortunate that these periodic replacements of the lamina sheath with its cusps have never been followed through during the life span of a lamprey in captivity². Thus there is no exact information as to how many times replacement of the external corneous covering of the infraoral lamina occurs.

In the spring of 1960 we tried to keep newly transformed *P. marinus* in captivity. Unfortunately, due to an inadequate water supply, we lost our experimental animals. Thus, to continue our studies we were limited to observations on formalin-preserved lampreys. The main points of interest were: (1) observation on growth, i.e., the increase in size of the infraoral lamina with the growth of the lampreys; (2) establishing the different types of the lamina; and (3) studying the order of succession of different types of lamina.

GROWTH OF THE INFRAORAL LAMINA

Our specimens show clearly that the width of the infraoral lamina, irrespective of its type, increases directly with the size of the lamprey.

LAKE ERIE AREA

During 1957-1959 lampreys from Lake Erie proper were collected principally off Port Maitland and Port Burwell (Table I). From the 130-149 to the 550-599 mm length class the average increase in size of the infraoral lamina was from 4.8 to 13.8 mm (Table XIII). There was some overlap in width of the lamina among individuals from neighbouring length classes. The extreme range of sizes was from 4.5 mm in several newly transformed lampreys up to 16.5 mm in a female 525 mm long, i.e., about a 4-fold increase. However, the largest lampreys do not necessarily possess the largest laminae. In our largest specimen from Lake Erie, a female 635 mm long, the width of the lamina was only 15 mm.

Samples from Lake Erie collected during 1957-59 differ greatly from lampreys obtained in 1960 from Big Creek, a principal lamprey spawning stream of that lake (Table XIII). The average width of the lamina in immature specimens was always less than in spawning individuals of corresponding lengths. This doubtless results from the shrinkage of the body of the mature lampreys, so that their lamina widths correspond to those of immature individuals of larger size.

LAKE SENECA AREA

Two samples were obtained from this area. One consisted of spawning lampreys from the Catherine Creek, and the other of immature specimens taken in the lake proper. This material shows results similar to those described for Lake Erie (Table XIV). In both localities spawning lampreys have wider infraoral lamina than immature specimens of corresponding sizes.

²The natural life-span of transformed anadromous *P. marinus* is about two years (Vladykov, 1949). Very similar longevity has been observed in landlocked specimens (Applegate, 1950).

Catherine Creek lampreys have on the average larger laminae than Big Creek specimens of corresponding sizes. This difference may be attributed to local conditions or, what is more likely, to a differing degree of maturity of each group of lampreys. Those from Big Creek (Tables XII, XIII) were pre-spawning specimens, while lampreys from Catherine Creek (Table XIV) were actually spawning and some were even spent. So the shrinkage in the body length of the Catherine Creek specimens had reached its maximum. The following schedule illustrates the importance of length shrinkage (sexes combined):

Length class mm	Average width of infraoral lamina, mm	
	Big Creek	Catherine Creek
250-99	9.0	9.8
300-49	9.8	10.9
350-99	10.8	12.4
400-49	12.0	13.2
450-99	13.5	—

In Catherine Creek lampreys the width of the infraoral lamina of any length-class corresponds almost exactly to that of Big Creek specimens in the next higher length class.

VARIATION WITH SEX

Lampreys from the Lake Erie area (Table XIII) do not show any difference between sexes in respect to the width of infraoral lamina. This might result from the fact that our material was obtained throughout four different years and probably represented several distinct populations, each spawning in different brooks.

In Lake Seneca apparently there is only one spawning area (Catherine Creek), where all our mature lampreys were collected. The immature specimens caught during the same year in the lake proper probably belong to the same population. This explains the uniformity of the Seneca material. In the Seneca lampreys males have on the average, larger infraoral laminae than females, both when immature and when spawning.

THE "ROSEBUD" INFRAORAL LAMINA

The rosebud lamina (*r*) is the most striking type. Its cusps are very small, and the cusp-row, practically of the same size as in newly-transformed specimens, represents only about 50% of the laminar width, while in other types the cusp-row is at least 72% of laminar width (Table II). Below the cusps on the horny (or corneous) part of the lamina several horizontal lines are present which do not occur on other types of infraoral lamina. These horizontal lines represent stratification of the horny sheath. We believe that during the growth of the animal the original horny sheath of the infraoral lamina of the newly-transformed

lamprey is not sloughed off and replaced by a new larger one (as in the case of other types of the infraoral lamina), but rather is retained for some time. This original lamina (or rather its exterior sheath) grows in width and height by adding extra rings around its lower edge. The pronounced growth of the lower section of the infraoral lamina, while the original cusps remain unaltered, results in a formation of the rosebud type (Fig. 4e, 4g). Histological studies have been undertaken to find out the exact method of rosebud lamina formation, whose results will be published in a subsequent paper.

FREQUENCY ACCORDING TO SIZE OF LAMPREY

Among 288 Erie lampreys, irrespective of sex, rosebud laminae were found only in half-grown specimens ranging in length from 182 to 551 mm. The highest frequencies were in length classes 250-99 mm (94%), 300-49 mm (80%), and 350-99 mm (69%) (Table III). In 58 young specimens 130-180 mm in length no rosebuds were present. Similarly, among 113 large lampreys 400-635 mm in length, only 11 cases (about 10%) of rosebuds were observed. A comparable situation existed in the Seneca lampreys (Table VI).

FREQUENCY ACCORDING TO STAGE OF MATURITY

By arranging the Erie specimens according to stages of maturity, we find that 15% rosebuds are present in Stage 0 immature lampreys, 48% in Stage 1, and 24% in Stage 2. Other details are found in Table VIII.

Among the Seneca specimens rosebud laminae were confined to the immature group, and involved 12 lampreys out of 26 (Table IX). No rosebuds were present in 122 spawning individuals.

The occurrence of different types of infraoral lamina in *Petromyzon marinus* from the five localities studied is summarized in Table X. Among Père Marquette lampreys, which represented an early spawning run, only one specimen had the rosebud type while the remaining 86 had other types of infraoral lamina. Rosebuds were completely absent among lampreys in advanced spawning conditions from Big Creek and Catherine Creek.

Altogether 92 specimens with rosebuds were observed during the present study. Grouping them by lamprey length classes irrespective of localities (Table XI), almost 73% fall within the range 250-400 mm. Among specimens longer than 500 mm, only 2 individuals carried rosebuds (about 2%). Rosebuds were equally rare (about 3%) among specimens smaller than 200 mm. Thus, rosebud laminae were characteristic of the half-grown lampreys only, while the young and adults possessed other types.

OTHER TYPES OF LAMINA

The other types of infraoral lamina, *inclined* (*i*), *normal* (*n*) and *intermediate* (*i-n*), differ only in the direction of the cusps, being quite similar otherwise. The cusp-row in these types occupies 86-90% of the laminar width (Table II). Their cusps are much stronger and sharper than in the rosebud type (Fig. 1).

YOUNG LAMPREYS. Among the Erie material there were 13 newly transformed lampreys 130-149 mm in length, all of which possessed a normal infraoral lamina. In the 150-199 mm class also the normal type was most common (73%).

HALF-GROWN LAMPREYS. As already mentioned, rosebud is the characteristic type of infraoral lamina in half-grown lampreys (Tables III-XI).

ADULT LAMPREYS. Among 123 large Erie lampreys 400 to 635 mm long, 101 specimens (82%) had inclined laminae. Many of these were still immature individuals (Tables III, VIII). Equally high incidence (84%) of the inclined type of lamina was observed in Père Marquette lampreys caught in April (Tables VII, X). Among lampreys from Big Creek, many of which were almost ready to spawn (Stage 4), the incidence of the inclined type was much lower, only 56% (Table X).

SPAWNING LAMPREYS. About half of the sample from Big Creek consisted of lampreys in an advanced stage of maturity (Table XII); thus many of these specimens have replaced the inclined type of lamina by other types: 28% had the intermediate type, 16% the normal type. On the other hand, spawning Catherine Creek lampreys had over 80% normal laminae (Table X) and none of the inclined type at all.

ORDER OF SUCCESSION OF TYPES OF INFRAORAL LAMINA

In addition to direct observation on types of infraoral lamina present in lampreys of different sizes, we tried to remove the existing outer sheath of the lamina to study the underlying cusps. The existing sheath is called in this paper the "old set", and the underlying one the "new set" (Table XV). In many preserved specimens, especially of spawning lampreys, the old set of infraoral lamina was ready to be sloughed off. In nature, spawning specimens regularly replace the old sets by new ones.

Among half-grown specimens, where the old set is of the rosebud type, it also was easily detachable. However, a forcible removal of the old set of other types of lamina in half-grown specimens, and especially in newly-transformed lampreys, presented difficulty, with the result that the old set was often damaged. The use of a dissecting needle and a binocular microscope was helpful.

There is little published information regarding the manner and sequence of tooth replacement in lampreys. For the genus *Ichthyomyzon*, Hubbs and Trautman (1937, p. 29) state that "each new tooth, formed as the core of its predecessor, is the image of the former tooth which is sloughed off as a hollow corneous structure". Ivanova-Berg (1933, p. 27) observed that in spawning *Lampetra fluviatilis* the infraoral cusps were blunt, while those in half-grown specimens were sharp.

In our spawning *Petromyzon marinus*, the old set of infraoral lamina was very often worn out, while the new set always carried sharp cusps. On several

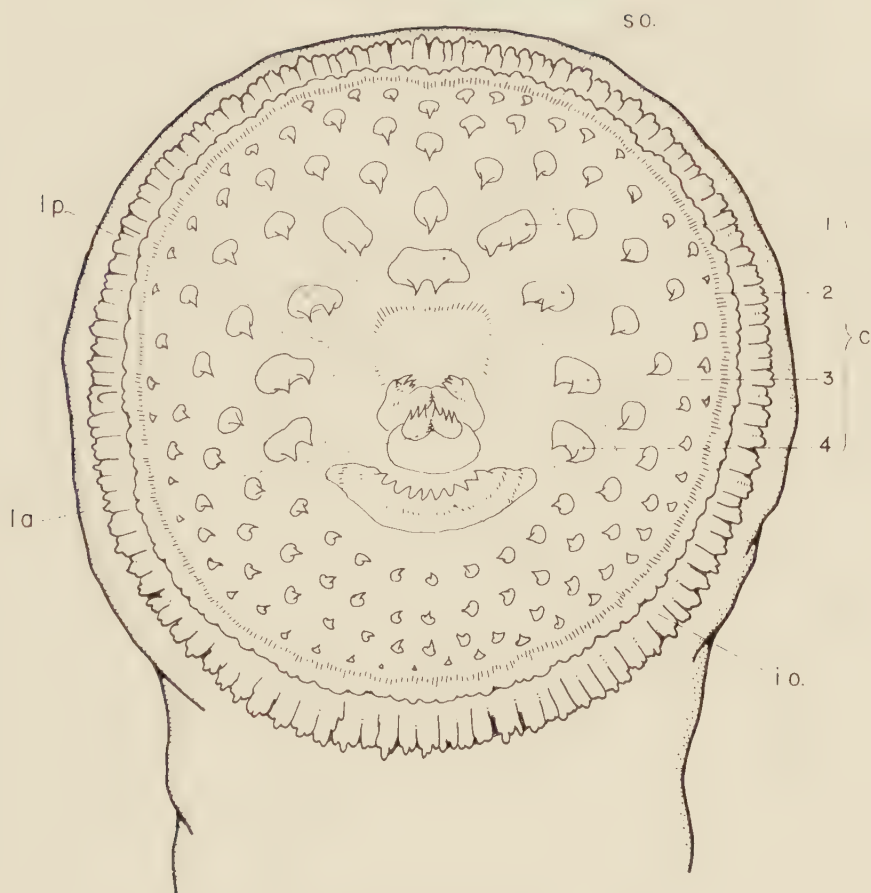


FIG. 1. Schematic drawing of the disc and dentition in the landlocked sea lamprey, *Petromyzon marinus*. The significance of the abbreviations used in this drawing is as follows:

- c.—Four circumorals or enlarged laterals.
- i.o.—Infraoral lamina or infraoral cusps.
- l.a.—Transverse, or anterior, lingual lamina.
- l.p.—Longitudinal, or posterior, lingual laminae.
- s.o.—Supraoral lamina or supraoral cusps.



FIG. 2. Examples of the 4 types of infraoral lamina ($\times 5.4$). From top downward:

Rosebud—♀, 551 mm, Lake Erie, 1960.

Inclined—♀, 450 mm, Big Creek, 1960.

Intermediate—♀, 525 mm, Lake Erie, 1959.

Normal—♂, 695 mm, Minho River, Portugal, 1959.

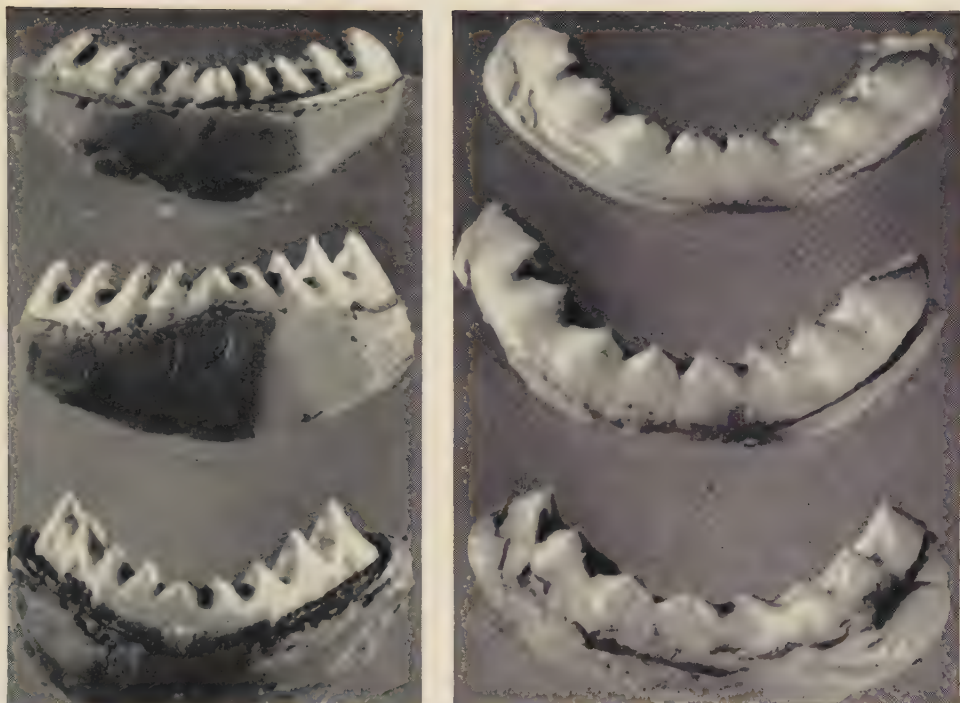


FIG. 3. Successive sets of sheaths taken from the same lamprey ($\times 4.4$), the oldest (functional) set at the top.

Left: ♀, 475 mm, Big Creek, 1960. *Top*—inclined; *middle*—inclined; *bottom*—normal.

Right: ♀, 497 mm, Lake Erie, 1959; *Top*—normal; *middle*—normal; *bottom*—normal.

FIG. 4. (colour plate opposite). Double sets of infraoral laminae ($\times 2$). Functional set *above*, new set *below*, except in (a) where positions are reversed.

- (a) Inclined (old set) and intermediate (new set): ♂, 380 mm, Big Creek, 1960.
- (b) Both normal; ♂, 548 mm, Lake Erie, 1957.
- (c) Both normal: ♂, 465 mm, Lake Erie, 1958.
- (d) Both inclined: ♂, 365 mm, Catherine Creek, 1959.
- (e) Rosebud above, inclined below: ♂, 458 mm, Père Marquette River, 1958.
- (f) Inclined above, intermediate below: ♀, 399 mm, Père Marquette River, 1958.
- (g) Rosebud above, inclined below: ♂, 380 mm, Lake Erie, 1959.
- (h) Inclined above, intermediate below: ♂, 411 mm, Chocolay River, Lake Superior, 1958.

(a)



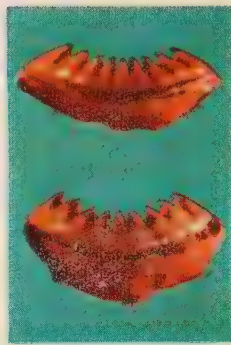
(b)



(c)



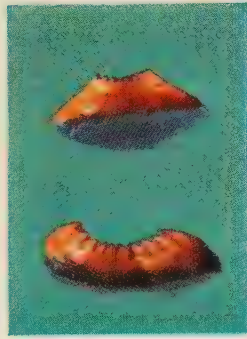
(d)



(e)



(f)



(g)



(h)

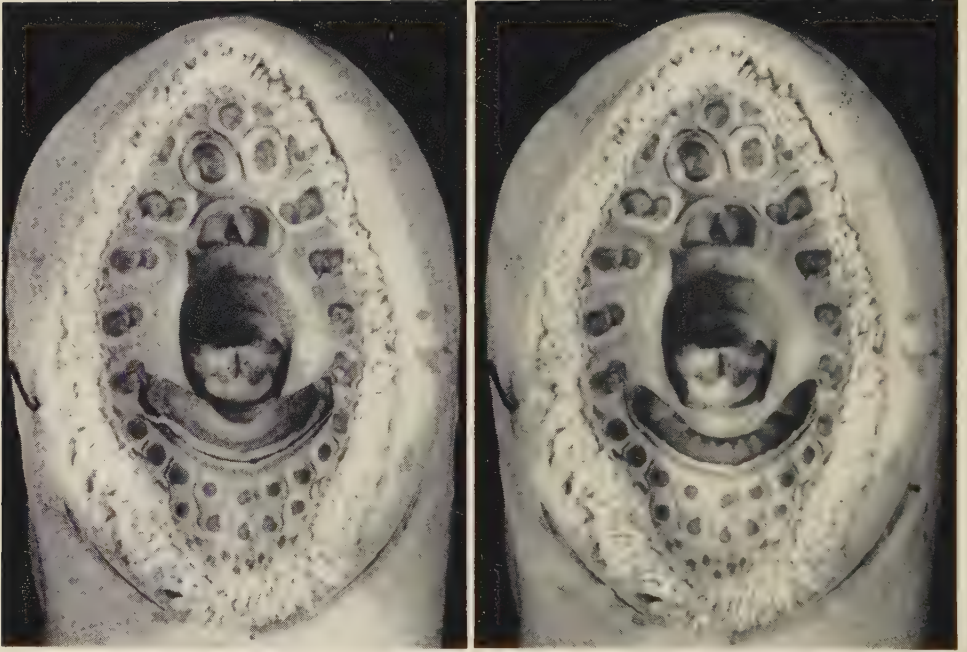


FIG. 5. Oral disc ($\times 2$) of ♀ lamprey No. 2157, 389 mm, Lake Erie, 1957.
Left: as captured, with rosebud lamina.
Right: inclined lamina exposed by removal of the rosebud.



FIG. 6. Oral disc ($\times 10$) of a newly transformed lamprey, 139 mm long, Carp Lake River, Michigan, February 1960. Infraoral lamina of the normal type.



FIG. 7. Oral disc ($\times 3$) of a spawning ♂ lamprey, 389 mm long, Catherine Creek, Seneca Lake, N.Y., May 1959. Infraoral lamina of the normal type.

occasions, when collected specimens were properly handled previous to preservation in formalin, we observed that beneath the first new set, a second new set was present with equally sharp cusps (Fig. 3). We are convinced that in nature all spawning sea lampreys have two new sets of the infraoral lamina. Apparently a similar situation, in the case of other teeth, was observed in spawning anadromous *P. marinus* in France by Fontaine (1958, p. 73), who wrote that "nous avons fréquemment constaté, chez la Lamproie marine, la présence sur les grosses dents de 3 coiffes cornées emboîtées".

FREQUENCY OF REPLACEMENT OF CORNEOUS SHEATHS

There is no definite information available as to the frequency of replacement of corneous sheaths of the infraoral lamina. A new sheath is always somewhat larger than the preceding old sheath. This can help us to evaluate, at least approximately, the number of sheath changes throughout the life-span.

We were able to measure with fine dividers the old and new laminar sheaths of 76 Big Creek lampreys. The differences in width are summarized below:

Difference, mm	0-0.4	0.5-0.9	1.0+
Occurrence, %	48.7	47.4	3.9

Table XIII shows that the width of the infraoral lamina increases from 4.5 mm in the newly-transformed lamprey to about 14 mm in grown-up individuals. Thus, the difference between these extremes is about 10 mm. If the absolute increase in the size of the lamina with each new replacement of the corneous sheath is uniform, then we can speculate as to how often a lamprey replaces its corneous sheaths. If at each replacement the width of the lamina increases by 0.5 mm on the average, the number of replacements should be about 20. If the increase is only 0.25 mm, the number of replacements is 40. The true figure must lie between these two—possibly close to 30.

ORDER OF SUCCESSION

In order to understand better the succession of different types of infraoral lamina, we studied in detail the old and new sets in 210 specimens of *Petromyzon marinus* from several localities and in different stages of maturity (Table XV).

YOUNG LAMPREYS. In 10 specimens with the normal type of lamina in the old sets, the new sets were represented mainly (90%) by normal and intermediate types. However these new sets consisted of only a soft core, the outside sheathing of which was not corneous as yet. Thus, a future new set could be different from the one in the process of formation, as mentioned in Table XV.

HALF-GROWN LAMPREYS. Among 28 semi-adult specimens with old sets of the rosebud type, the new sets were invariably of the inclined type.

ADULT LAMPREYS. Among grown-up lampreys with old sets of the inclined type, the kind of new set underneath varies with stage of maturity. Among 47 Erie specimens, nearly 92% of the new sets were inclined again. Père Marquette lampreys, more advanced in maturity, had less than 15% of inclined sets, while intermediate and normal types were represented by 43% each. Among

Big Creek lampreys, many of which were ready to spawn, the inclined type among the new sets was only about 7%, and the normal type was most frequent (52%) in the sample. The spawning Catherine Creek lampreys did not have an inclined type among the new sets, and the normal type was present in over 83% of specimens.

SPAWNING LAMPREYS. The small number of available specimens shows that the intermediate type of lamina is replaced mainly (83%) by the normal type. The normal type is replaced invariably by a normal type again (Table XV). It should be added that in spawning lampreys the cusps of the normal infraoral lamina are usually narrow, hence farther apart, and their tips are often bent. In feeding adult landlocked sea lampreys, the cusps of the normal lamina are rather broad and wedge-like. The latter type of cusp is particularly characteristic of anadromous *P. marinus* (Fig. 2, bottom).

SUMMARY

1. Detailed study was made of 630 landlocked *Petromyzon marinus* from three lake areas: Erie, Superior, and Seneca.

2. The three main types of infraoral lamina were: *rosebud* (*r*), *inclined* (*i*), and *normal* (*n*), the latter including an intermediate type (*i-n*).

3. Newly-transformed and young lampreys, smaller than 180 mm, have the normal type of lamina. The rosebud lamina is a characteristic of half-grown specimens, being found most frequently among lampreys 250–400 mm in length (Table III). In adults, feeding in lakes, the predominant type is the inclined lamina. In spawning specimens the normal lamina is most characteristic.

4. The old corneous sheaths of inclined, intermediate, or normal infraoral laminae can be succeeded not only by different types, but also by a new one of the same type (Table XV). On the other hand, we have never seen a lamprey in which the old lamina sheath of the rosebud type was succeeded by a new set of rosebud.

5. Inclined infraoral laminae can appear successively several times before they are finally replaced by intermediate or normal type.

6. In some mature lampreys the intermediate type of lamina can be succeeded again by the same type, instead of the normal type. These two types are very similar in appearance, and are found concurrently (Fig. 4f, 4h).

7. Irrespective of the type, the size (width) of the infraoral lamina increases slowly with successive replacements of the previous corneous sheaths, the extreme range observed being from 4.5 to 16.5 mm (Table XIII).

8. It is not definitely known how often a sea lamprey, during its life-span, replaces the corneous sheaths of its teeth, but the average increase in width between successive laminae suggests that there are about 30 changes.

9. The number of cusps on the first set of the infraoral lamina is always repeated in the consecutive new sheaths.

10. There is a tendency for successive types of infraoral lamina to have a pattern of replacement which permits the tips of the cusps to spread further apart with each new corneous sheath. Beneath the small parallel cusps of the rosebud are found larger cusps of the inclined lamina, the tips of which are still cramped and directed towards the centre. In an intermediate type, the cusps are spread farther apart and are almost parallel to one another; in the normal type they are even more so (Fig. 4b).

11. Landlocked *Petromyzon marinus* exhibit the following changes in the infraoral lamina. The first set is normal followed only once by a rosebud, which is then succeeded several times by inclined; during the spawning period the inclined type is replaced at least twice by the intermediate type or, more frequently, by normal lamina. The first and the last sets are typically normal.

12. In gently handled spawning specimens (most probably in all of them), in addition to an old corneous sheath, two new sets of corneous sheaths were found, one beneath the other. It seems a "very extravagant luxury" for a mature lamprey to have even one extra corneous sheath, as this animal does not feed during spawning and dies very soon after.

ACKNOWLEDGMENTS

Much of this work was done during the senior author's seasonal employment by the Fisheries Research Board of Canada. Dr W. A. Kennedy, Director of the Board's London Biological Station, encouraged this investigation. Mr R. W. McCauley of the same Biological Station helped to obtain specimens from Big Creek. Mr W. J. Christie and Dr R. G. Ferguson, Biologists, Ontario Department of Lands and Forests, provided numerous specimens of sea lampreys from Lakes Ontario and Erie. Mr W. A. McGregor, Biologist, New York Conservation Department at Scottsville, N.Y., obtained very valuable material from the Lake Seneca area. Dr Mario Ruivo, Institute de Biologia Maritima, Lisbon, Portugal, kindly provided anadromous specimens of sea lamprey from northern Portugal. Mr S. U. Quadri, graduate student of our Department, helped in measuring of specimens. Mr G. A. Ben-Tchavtchavadze of the University of Ottawa expertly took the colour and black-and-white photographs. The drawing (Fig. 1) for this paper was done by Mr Paul I. Voevodine, artist of the Department of Fisheries, Quebec. To all these persons, the authors wish to express their most sincere thanks.

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TABLE I. Number and range of lengths of samples of landlocked sea lampreys.

Locality	Date	Collector	Lamprey samples			
			Males		Females	
			no.	mm	no.	mm
Lake Erie, Ontario	Summer-fall, 1957-59	R. G. Ferguson	84	143-548	153	130-635
Lake Erie, Ontario	Fall, 1960	R. G. Ferguson	19	295-572	32	342-551
Big Creek, Lake Erie, Ont.	May-June, 1960	Douglas Morris	60	276-546	47	292-523
Catherine Creek, Lake Seneca, N.Y.	May 20-29, 1959	W. A. MacGregor	71	275-430	51	266-401
Lake Seneca, New York	Fall, 1959	W. A. MacGregor	9	328-453	17	337-429
Père Marquette R., Michigan	April 10-24, 1958	W. E. Gaylord	60	322-512	27	354-531
Total	1957-1960		303	143-572	327	130-635

TABLE II. Definition of the different types of infraoral lamina in landlocked sea lampreys. "Width of the cusp row" is expressed as a percentage of the total laminar width.

Type	Specimens	Width of cusp row		Cusps	
		Range	Average	Size	Direction
Rosebud	no. 25	% 31.6-65.0	% 50.5	Small	Straight
Inclined	75	72.6-95.5	86.1	Large	Inclined toward the centre of the lamina.
Normal	35	83.3-95.7	90.2	Large	Straight and parallel to one another
Intermediate	23	79.5-96.0	88.6	Large	Outermost inclined toward centre of lamina, remainder straight

TABLE III. Frequency of different types of infraoral lamina according to lamprey length for *Petromyzon marinus* from Lake Erie, collected during 1957-59 and 1960 (sexes combined). Symbols for lamina types are as follows: *r*—rosebud; *i*—inclined; *i-n*—intermediate; *n*—normal.

Length	Specimens	Types of lamina			
		<i>r</i>	<i>i</i>	<i>i-n</i>	<i>n</i>
<i>mm</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>
130-49	13	—	—	—	13
150-99	59	3	4	8	44
200-49	20	8	5	2	5
250-99	16	15	1	...	...
300-49	25	20	4	...	1
350-99	32	22	10	...	...
400-49	38	5	33	...	...
450-99	39	4	31	...	4
500-49	40	1	33	...	6
550-99	5	1	3	...	1
635	1	...	1	...	...
Total	288	79	125	10	74

TABLE IV. Frequency of different types of infraoral lamina according to lamprey length, from Big Creek, 1960 (sexes combined). Symbols as in Table III.

Length	Specimens	Types of lamina		
		<i>i</i>	<i>i-n</i>	<i>n</i>
<i>mm</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>
250-99	5	4	...	1
300-49	25	16	6	3
350-99	27	19	5	3
400-49	15	7	4	4
450-99	30	13	14	3
500-49	5	1	1	3
Total	107	60	30	17

TABLE V. Frequency of different types of infraoral lamina according to lamprey length, from Catherine Creek, Lake Seneca, 1959 (sexes combined). Symbols as in Table III.

Length	Specimens	Types of lamina		
		<i>i</i>	<i>i-n</i>	<i>n</i>
<i>mm</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>
250-99	10	...	1	9
300-49	57	6	3	48
350-99	47	...	9	38
400-49	8	4	1	3
Total	122	10	14	98

TABLE VI. Frequency of different types of infraoral lamina according lamprey length in immature *P. marinus* from Lake Seneca, 1959 (sexes combined). Symbols as in Table III.

Length	Specimens	Types of lamina	
		<i>r</i>	<i>i</i>
<i>mm</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>
300-49	3	2	1
350-99	17	8	9
400-49	5	2	3
450-99	1	...	1
Total	26	12	14

TABLE VII. Frequency of different types of infraoral lamina according to lamprey length in specimens from Père Marquette River, 1958 (sexes combined). Symbols as in Table III.

Length	Specimens	Types of lamina			
		<i>r</i>	<i>i</i>	<i>i-n</i>	<i>n</i>
<i>mm</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>	<i>no.</i>
300-49	4	...	4	...	...
350-99	48	...	42	3	3
400-49	26	...	19	7	...
450-99	7	1	6	...	...
500-49	2	...	2	...	...
Total	87	1	73	10	3

TABLE VIII. Frequency of rosebud (*r*) and other types (*o*) of infraoral lamina in *P. marinus* from Lake Erie, collected in 1957-59 and 1960, grouped according to stage of maturity.

Length	Specimens	Stages of maturity (sexes combined)									
		0		1		2		3		Total	
		<i>r</i>	<i>o</i>	<i>r</i>	<i>o</i>	<i>r</i>	<i>o</i>	<i>r</i>	<i>o</i>	<i>r</i>	<i>o</i>
<i>mm</i>											
130-49	13	...	13	...	...	...	...	...	...	...	13
150-99	59	3	56	-	-	-	-	-	-	3	56
200-49	20	8	12	-	-	-	-	-	-	8	12
250-99	16	3	1	12	-	-	-	-	-	15	1
300-49	25	-	-	17	4	3	1	-	-	20	5
350-99	32	-	-	13	4	9	6	-	-	22	10
400-49	38	-	-	3	20	2	13	-	-	5	33
450-99	39	-	-	3	17	-	11	1	7	4	35
500-49	40	-	-	-	5	-	16	1	18	1	39
550-99	5	-	-	-	2	1	-	-	2	1	4
635	1	-	-	-	-	-	-	-	1	-	1
Total	288	14	82	48	52	15	47	2	28	79	209

TABLE IX. Frequency of different types of infraoral lamina in *Petromyzon marinus* from the Lake Seneca area, 1959. I=immature, taken in Lake Seneca in autumn, 1959; S=spawning specimens collected in Catherine Creek, spring, 1959.

Length	Infraoral lamina types									
	Rosebud		Inclined		Intermediate		Normal		Total	
	I	S	I	S	I	S	I	S	I	S
<i>mm</i>										
250-99	-	-	-	-	-	1	-	9	-	10
300-49	2	-	1	6	-	3	-	48	3	57
350-99	8	-	9	-	-	9	-	38	17	47
400-49	2	-	3	4	-	1	-	3	5	8
450-99	-	-	1	-	-	-	-	-	1	-
Total, no.	12	-	14	10	-	14	-	98	26	122
Total, %	46.0	-	54.0	8.2	-	11.5	-	80.3	100	100

TABLE X. Frequency of the different types of infraoral lamina from five localities (sexes combined). Based on Tables III-VII; symbols as in Table III.

Locality	Date	Length <i>mm</i>	Maturity	Specimens <i>no.</i>	Types of lamina			
					<i>r</i>	<i>i</i>	<i>i-n</i>	<i>n</i>
Lake Erie	Summer-Fall 1957-60	130-635	Immature (Stages 0-3)	288	% 27.4	% 43.5	% 3.5	% 25.6
Lake Seneca	Fall, 1959	328-453	Immature (Stages 0-2)	26	46.1	53.9	0	0
Père Marquette River	April, 1958	322-531	Early spawning run (Stage 3)	87	1.2	84.0	11.5	3.3
Big Creek, Lake Erie	May-June, 1960	276-546	Pre-spawning (Stage 4)	107	0	56.0	28.0	16.0
Catherine Creek, Lake Seneca	May, 1959	266-430	Spawning (Stages 5-6)	122	0	8.1	11.4	80.5

TABLE XI. Frequency of the rosebud type of infraoral lamina according to size of lamprey. Specimens of both sexes from three different localities are combined, data from Tables III-VII.

Length	Frequency	
<i>mm</i>	<i>no.</i>	%
150-99	3	3.3
200-49	8	8.7
250-99	15	16.3
300-49	22	23.9
350-99	30	32.6
400-49	7	7.6
450-99	5	5.4
502	1	1.1
551	1	1.1
Total:	92	100.0

TABLE XII. Frequency of the different widths of intestine in *Petromyzon marinus* from three spawning areas (sexes combined).

Locality	Date	Specimens	Width of intestine (<i>mm</i>)							
			1.5-3	4-6	7-9	10-12	13-15	16-18	27	Av.
Père Marquette River, Lake Michigan	April, 1958	87	% 0	% 19.5	% 42.5	% 25.3	% 10.3	% 1.2	% 1.2	<i>mm</i> 9.0
Big Creek, Lake Erie	May-June, 1960	107	33.7	62.6	3.7	0	0	0	0	3.9
Catherine Creek, Lake Seneca	May, 1959	122	97.6	1.6	0.8	0	0	0	0	2.4

TABLE XIII. Increase in the width of infraoral lamina with size and stage of maturity of *Petromyzon marinus* from Lake Erie area, 1957-1960.

Length	Sex	Immature, Lake Erie, 1957-59			Spawning, Big Creek, 1960		
		Specimens	Width of lamina		Specimens	Width of lamina	
			Range	Av.		Range	Av.
mm		no.	mm	mm	no.	mm	mm
130-49	♂	4	4.5-5.5	4.8			
	♀	9	4.5-5.5	4.8			
150-99	♂	20	5.0-5.5	5.2			
	♀	39	4.5-6.5	5.4			
200-49	♂	6	5.5-9.0	7.1			
	♀	14	5.0-7.5	6.3			
250-99	♂	6	7.0-9.0	7.7	4	8.5-9.0	8.9
	♀	9	7.0-9.5	8.1	1	9.5	9.5
300-49	♂	10	7.5-10.0	9.1	16	8.5-11.0	9.7
	♀	11	8.0-10.0	9.0	9	8.5-11.0	9.9
350-99	♂	10	9.0-11.5	10.1	14	9.0-12.0	10.8
	♀	16	8.0-12.0	10.1	13	9.5-12.0	10.7
400-49	♂	9	9.0-14.0	11.2	5	11.0-13.0	12.3
	♀	13	9.5-12.0	10.9	10	11.0-13.0	11.9
450-99	♂	6	10.0-13.5	11.9	19	11.5-15.0	13.6
	♀	15	10.0-15.0	12.7	11	12.0-14.5	13.4
500-49	♂	12	13.0-16.0	14.7	2	13.0-13.5	13.3
	♀	20	11.5-16.5	13.3	3	13.0-16.0	14.5
550-99	♀	2	13.0-13.5	13.3			

TABLE XIV. Increase in the width of infraoral lamina with size and stage of maturity, Lake Seneca area, 1959.

Length	Sex	Immature (L. Seneca)			Spawning (St. Catherine Creek)		
		Specimens	Width		Specimens	Width	
			Range	Av.		Range	Av.
mm		no.	mm	mm	no.	mm	mm
250-99	♂	0	...	...	2	9.5-11.0	10.3
	♀	0	...	...	8	8.0-11.0	9.7
300-49	♂	2	9.0-11.0	10.0	18	10.5-13.0	11.8
	♀	1	...	8.0	28	8.5-12.0	10.3
350-99	♂	5	8.0-11.0	10.9	35	11.5-14.0	12.6
	♀	12	7.5-11.0	9.5	7	11.0-11.5	11.2
400-49	♂	2	10.5-12.0	11.3	5	12.5-14.0	13.2
	♀	4	9.0-11.0	10.0	...	...	...

TABLE XV. Order of succession of different types of infraoral lamina, according to size and sexual maturity, in specimens of *Petromyzon marinus* from different localities (sexes combined). Symbols as in Table III.

Locality ^a	Maturity ^b	Length	Specimens	Succession of lamina types				
				Old set	New set			
					<i>r</i>	<i>i</i>	<i>i-n</i>	<i>n</i>
		<i>mm</i>	<i>no.</i>		<i>%</i>	<i>%</i>	<i>%</i>	<i>%</i>
L. Erie	Young ^c	164-193	10	<i>n</i>	0	100.0	40.0	50.0
L. Erie	Semi-adult	227-551	28	<i>r</i>	0	100.0	0	0
L. Erie	Adult	346-572	47	<i>i</i>	0	91.5	8.5	0
Père Marquette R.	Pre-spawning	322-531	63	<i>i</i>	0	14.4	42.8	42.8
Big Creek	Pre-spawning	276-548	54	<i>i</i>	0	7.4	40.7	51.9
L. Erie	Adult	404-548	6	<i>i-n</i>	0	0	83.4	16.6
Catherine Ck.	Spawning	275-383	6	<i>i-n</i>	0	0	16.6	83.4
Catherine Ck.	Spawning	291-338	6	<i>n</i>	0	0	0	100.0

^aLocalities and dates of collection are as in Table I.

^bDegrees of maturity on this table correspond approximately to the following stages of the numerical system: young (0-1), semi-adult (1-2), adult (2-3), pre-spawning (3-4), spawning (5-6).

^cIn young specimens, sheaths of new sets of infraoral laminae were not corneous as yet.

Ocean Temperatures and Their Relation to Albacore Tuna (*Thunnus germon*) Distribution in Waters off the Coast of Oregon, Washington and British Columbia¹

BY DAYTON L. ALVERSON²

ABSTRACT

Commercial albacore fishing offshore from Oregon, Washington and British Columbia, occurs during summer months when offshore surface water temperatures exceed 58°F (14.4°C). Fishermen have established 58°F (14.4°C) surface temperature as an indicator of "tuna water", and this rule-of-thumb relationship for surface water temperatures and albacore has generally been substantiated by total catch versus temperature records made during albacore investigations. Catch-per-hour data are also in accord with this general thesis. Catch-per-unit-effort data, however, do not indicate as marked a decline in availability at temperatures between 54 and 58°F (12.2–14.4°C) as might be interpreted from qualitative observations. With the exception of one albacore caught by a gillnet in 1956, all albacore have been taken in Bureau investigations where surface temperatures exceeded 54°F (12.2°C) and highest catch rates were obtained between 58 and 61°F (14.4–16.1°C). As the thermocline depth averages about 60 feet (18.3 m) in the summer months offshore from the Pacific Northwest states and temperatures are all well below 50°F (10°C) at the bottom of the thermocline, albacore probably inhabit only the overlying (mixed layer) lens of warm oceanic water. Concentrations of albacore appear to occur along the interface of the warm oceanic waters and the cooler waters adjacent to the coast.

FOLLOWING the inception of albacore fishing contiguous to the States of Oregon and Washington and the Province of British Columbia (about 1937), northwest fishermen quickly established an empirical relationship between surface water temperature and the occurrence of albacore. The expression "tuna water" used by northwest fishermen refers to the typical deep blue oceanic water having surface temperatures equal to or greater than 58°F (14.4°C).

Observations made during numerous albacore investigations in the north-eastern Pacific Ocean (Powell and Hildebrand, 1950; Powell *et al.*, 1952; Partlo, 1950) generally substantiate this relationship, and concentrations of albacore have seldom been observed or harvested during research cruises in areas where surface temperatures fall much below 58°F (14.4°C). Powell *et al.* (1952) report surface water temperature as one of the limiting factors governing the occurrence of albacore adjacent to the continent of North America. The depth of the lens (mixed layer) of warmer water, > 57°F (> 13.9°C) is also regarded as an important determinant of the occurrence of albacore (Powell *et al.*, 1952; Powell and Hildebrand, 1950).

Although 58°F (14.4°C) surface water temperature has proved a reliable indicator of the lower limit for occurrence of commercial quantities of this species, albacore have been captured in areas where surface temperatures were as low as

¹Received for publication June 24, 1961.

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54°F (12.2°C) (Powell *et al.*, 1952; Neave and Hanavan, 1960). In a few instances relatively good fishing has been reported at temperatures to 56° (13.3°C).

Water colour has also been used by fishermen as a general guide to "tuna water" and it has been reported by various investigators to bear some relationship to successful albacore fishing, i.e., albacore are not normally taken adjacent to the Pacific Northwest coast in the greenish inshore waters which overlie the continental shelf and slope (Powell and Hildebrand, 1950).

It is the objective here to review and summarize observations which appear pertinent to the occurrence and distribution of albacore in waters adjacent to the States of Oregon, Washington, and the Province of British Columbia, and to evaluate quantitatively, by measure of catch per unit of effort, fishing success at various surface water temperatures.

BACKGROUND

The albacore fishery in the Pacific Northwest normally begins in mid-July, peaks in August and September, and tapers off during late October. In some years fishing has continued into early November. Fishing operations are geared to get under way in mid-summer and the fishermen constantly check offshore water temperatures. Following reports of warm or "tuna water" scouting for tuna quickly commences.³ In a typical year the fishery will first begin in the area between Newport and Astoria, Oregon, and gradually extend northward to areas off Washington and southern Vancouver Island. The northern extent of reported commercial operations has been offshore from the northern Queen Charlotte Islands. Commercial fishing generally occurs in waters within 50 to 200 miles (81–322 km) off the coast.

REVIEW OF PAST EXPLORATIONS

Since 1949 the U.S. Bureau of Commercial Fisheries has conducted 5 exploratory fishing cruises to determine the general distribution patterns of albacore in waters contiguous to Washington, Oregon, British Columbia, and Alaska (Fig. 1). During the explorations water temperature, thermocline depth, and water colour and availability of albacore were recorded. A summary of these observations is shown in Table I.

Surface water temperatures in areas where albacore were caught ranged from 54 to 63°F (12.2–17.2°C). These temperature ranges for albacore distribution in the northeastern Pacific area are in accord with observations made by Neave and Hanavan (1960), and the range 58 to 60°F (14.4–15.6°C) given by Partlo (1950) for the best catches of albacore taken off Vancouver Island. The depth of the thermocline in areas where good catches were taken ranged between 50 and 75 feet (15.2–22.9 m) with an average of about 60 feet (18.3 m).

³Temperature data are provided to the fishing fleet by offshore fishing craft engaged in other fisheries. Surface temperature charts issued by U.S. Bureau of Commercial Fisheries Biological Laboratory at San Diego, California are now in use.

The blue colour of water which has been associated with good albacore fishing by various authors is another empirical relationship established by fishermen exploiting tunas from Pacific Northwest ports. The decrease in availability of albacore in green waters is well documented (Powell *et al.*, 1952; Powell and Hildebrand, 1950). Fair catches have, however, been reported in blue-green water, although the blue oceanic waters have constantly yielded best catches. Water colour itself is probably unimportant. The transition from blue oceanic water to coastal green water generally demarks the inshore limit of water having surface temperatures greater than 57°F (13.9°C). The temperature gradient is normally relatively sharp at the boundary (blue to green) between oceanic and coastal waters.

It should be noted that this rule-of-thumb relationship (58°F or 14.4°C = tuna water) is one of negative rather than positive association, i.e., waters with surface temperatures less than 58°F are not likely to yield commercial quantities of albacore, but on the other hand, 58°F surface temperatures or greater do not necessarily insure successful albacore fishing.

It has been suggested by Powell *et al.* (1952) and Radovich (1960) that distribution of albacore within the temperature regime that the species normally inhabits in the Pacific Northwest area is probably associated with feeding or other biological determinants rather than being temperature dependent. Appraisal of the surface water temperature-albacore relationship for past explorations has been based on the availability of the species to troll or gillnet gear fished in waters of different temperature ranges. Published data for these investigations as well as other investigations (Partlo, 1950; Craig and Graham, 1961) have shown either percentage catch or absolute catch in numbers of albacore for specified

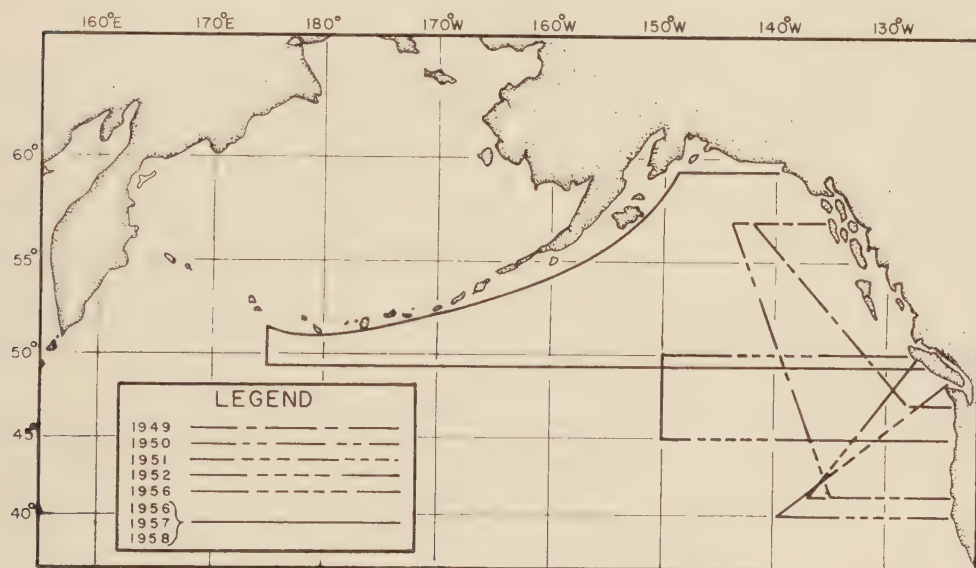


FIG. 1. Areas surveyed by years.

TABLE I. Surface water temperatures for albacore catches, best fishing temperatures, and water colour reported in areas of best fishing for five exploratory cruises in the northeastern Pacific Ocean.

Authors	Year	Temperature ranges				Thermocline depth, best catches		Water colour, best catches
		Occurrence		Good catches		feet	meters	
Powell and Hildebrand (1950)	1949	56.8-61	13.8-16.1	58-61	14.4-16.1	50	15.21	blue
	1950	54-62	12.2-16.7	57-61	13.9-16.1	60	18.29	blue
Powell <i>et al.</i> (1952)	1951	58-62	14.4-16.7	58-61	14.4-16.1	...	...	...
Schaefers (1952)	1952	54-61	12.2-16.1	58-62	14.4-16.7	...	...	...
Schaefers (1953)	1956	55-63	12.8-17.2	58	14.4	50-75	15.21-22.86	...
Powell (1957)								...

temperatures. These indices have not accounted for expenditure of varying amounts of fishing effort.

To evaluate availability changes of albacore, data from the five exploratory operations conducted by the Bureau along with data from albacore catches taken during North Pacific salmon studies in the years 1956, 1957, and 1958, were analyzed to yield information on the catch-per-hour fishing by 2-degree F (1.1-degree C) temperature intervals of surface water. Units used were catch-per-lure-hour and catch-per-shackle-hour, where a lure-hour equalled one hour's fishing with a single trolling lure and a shackle-hour equalled one hour's fishing with a 50-fathom (91-meter) shackle of gillnet.

RESULTS

Hours fished and catch-per-hour fishing by gear are shown for each cruise in Tables II through IV. These data are summarized in Table V which gives the mean value of catch-per-hour for the five exploratory cruises plus albacore gillnet catches taken during high seas salmon studies for the years 1956, 1957 and 1958. Catch rates for trolling were highest when temperatures ranged between 58 and 61°F (14.4-16.1°C) and in all years, with the exception of 1956, the catch rates fell rapidly at temperatures below 58°F. These data generally support catch-temperature data tabulated without regards to fishing effort,

TABLE II. Trolling catch per unit of fishing effort by year and surface temperature ranges. (Original data were recorded in degrees Fahrenheit.)

Temperature		1950		1951		1952		1956	
		Fish per 100 lure hours	Lure hours	Fish per 100 lure hours	Lure hours	Fish per 100 lure hours	Lure hours	Fish per 100 lure hours	Lure hours
°F	°C								
<52	<11.10	0	15	...	...	...	...	...	...
52-53	11.10-11.95	0	2235	0	266	0	320	0	153
54-55	11.96-13.05	5.45	550	0	140	0.08	1181	1.39	216
56-57	13.06-14.15	11.94	1617	0	847	1.09	1282	2.14	794
58-59	14.16-15.30	22.74	2164	1.13	2114	8.99	2057	0.89	1127
60-61	15.31-16.40	11.97	1011	6.12	1535	0	367	3.10	226
>61	>16.40	0	159	0	278	...	...	1.04	96

TABLE III. Total gillnetting effort (shackle hours) by year and surface temperature ranges.

Temperature		Total shackle hours fished						
		1949	1950	1951	1952	1956	1957	1958
°F	°C							
<52	<11.10	...	...	...	...	15,005	24,728	33,977
52-53	11.10-11.95	...	...	...	...	7,787	3,083	1,258
54-55	11.96-13.05	84	21	...	...	5,081	1,947	...
56-57	13.06-14.15	419	246	93	...	2,543	600	319
58-59	12.16-15.30	331	238	125	786	1,531	384	276
60-61	15.31-16.40	158	96	270	757	1,224	396	...
>61	>16.40	...	...	222	...	674	...	...

TABLE IV. Albacore gillnet catch per unit of fishing effort by year and surface temperature ranges.

Temperature		Number of fish per 100 shackle hours						
°F	°C	1949	1950	1951	1952	1956	1957	1958
<52	<11.10	...	...	...	...	0.01	0	0
52-53	11.10-11.95	...	...	...	...	0	0	0
54-55	11.96-13.05	0	0	...	...	0.18	0	...
56-57	13.06-14.15	9.78	67.07	0	...	0.43	1.50	0
58-59	14.16-15.30	18.43	19.75	2.40	0.25	0.91	0	0
60-61	15.31-16.40	39.24	33.33	5.92	0	0.16	0	...
> 61	> 16.40	...	...	4.05	...	0.44	...	...

TABLE V. Gillnet and trolling catch-per-unit-of-fishing effort (all years combined) by surface temperature ranges.

Temperature (°F)	Trolling		Gillnetting	
	Total lure hours fished	Fish $\times 10^2$ per lure hour	Total shackle hours fished	Fish $\times 10^2$ per shackle hour
<52	15	0	73,710	
52-53	2,974	0	12,128	0
54-55	2,171	1.57	7,049	0.13
56-57	4,959	5.34	3,801	4.87
58-59	7,793	9.91	3,340	1.98
60-61	3,291	8.63	2,743	1.82
61+	533	.19	896	1.34

but it is interesting to note that the indicated decline in availability at temperatures below 58°F is not nearly as sharp as that suggested by qualitative observations. For example, Powell *et al.* (1952) show that about 55% of the total catch was caught at temperatures from 58 to 59°F (14.4-15.0°C) and less than 10% of the total catch was taken at temperatures ranging from 56 to 57°F (13.3-13.9°C). Catch-per-hour fishing of trolling lures for 1950 shows a decline in availability for the 56-57°F (13.3-13.9°C) temperature range of about one-half that of the 58-59°F (14.4-15.0°C) temperature zone. Availability also appears higher in the next lower temperature zone of 54-55°F (12.2-12.8°C) than is evident from catch-temperature data alone.

The data for all years of gillnetting are strongly weighted by one excellent catch made in the Queen Charlotte Sound area in 1950 when surface temperatures were recorded at 57°F (13.9°C). For individual years best catches were normally made at temperatures of 58°F (14.4°C) or higher. In 1956 a single albacore was reported caught in a gillnet when the surface temperature was only 51°F (10.6°C).

DISCUSSION

The data reviewed generally substantiate the relationship suggested by other authors for surface water temperature and albacore occurrence in the Pacific Northwest. It is not surprising that the catch-per-effort data by temperature

increments does not indicate as rapid a decline in availability as might be interpreted from catch data alone. By concentrating in areas where albacore are most available the catches of commercial fishermen are strongly weighted to the temperature interval existing in areas of high availability.

Some evidence exists which suggests that albacore within the geographic area under discussion probably inhabit only those waters above the thermocline. This thesis, however, still lacks good supporting data. Powell *et al.* (1952) showed the majority of gillnet-caught albacore was taken in the upper portion of the nets and Powell and Hildebrand (1950) reported no albacore were captured by troll lines set to fish subsurface depths. Longline gear fished during Bureau explorations have also failed to take albacore in waters off the Pacific Northwest coast.⁴ If temperature limits the geographic distribution of albacore, then it may also be assumed a factor controlling bathymetric distribution. The limiting surface temperature appears to be about 54°F (12.2°C). As this temperature is well above that which is normally observed (about 46°F or 7.8°C) at the bottom of the summer thermocline structure in the Pacific Northwest, it is doubtful that the species sounds to depths greater than that of the thermocline.

It has been shown that the location of first catches of albacore off the Oregon coast accord well with the geographic position of the 57–58°F (13.9–14.4°C) isotherms. During late spring (June) the 27.5°F (14.2°C) isotherm generally parallels the Pacific coast of North America between San Diego and San Francisco, and then bends sharply to the west between San Francisco and Cape Blanco, Oregon. In mid-June this isotherm generally lies about 350 to 400 miles (564–644 km) west of Cape Blanco, Oregon. From July through September the 57°F (13.9°C) isotherm is found progressively northward. During mid- and late summer a pouch of warm water will normally develop adjacent to the coast of British Columbia with colder water lying both to the east and west of the pouch. Albacore catches are confined to the warmer water areas. Schaefers (1952) reports albacore can be taken with troll gear off Oregon prior to commercial fishing season by running west to the area of warm water. In three successive years (1950 through 1952) albacore were taken in Bureau explorations about 30 days prior to the start of the normal fishing season (mid-July). The albacore were caught shortly after exploratory fishing commenced in water where surface temperatures were greater than 57°F (13.9°C) at distances from 280 to 370 miles (451–569 km) offshore.

Throughout the fishing season commercial operations take place at distances from about 50 to 200 miles (81–322 km) seaward of the coast. It appears that albacore concentrate along the inter-face of the warmer oceanic waters and the cooler waters overlying the continental shelf and terraces. Exploratory fishing activities conducted at distances greater than 200 miles (322 km) seaward of the

⁴Acceptance of this evidence assumes that trolling and longline methods are effective methods of sampling albacore in subsurface waters and all areas of the gillnets are equally effective for capture of albacore. The use of longlines for capture of albacore is well documented in commercial and experimental fishing. Evidence of the vertical distribution of albacore, however, might be better defined by surface and subsurface gillnets, set above and below the thermocline.

coast during August and September have failed to take commercial concentrations of albacore, although surface temperatures were within the favorable range of 58–61°F (14.4–16.1°C). This is also substantiated by reports of albacore catches made by United States picket vessels (Johnson, 1961).

ACKNOWLEDGMENT

The author extends thanks to Gerald V. Howard, James H. Johnson, and Felix Favorite, U.S. Bureau of Commercial Fisheries, for review and suggestions for improvement of this manuscript. I am also indebted to the Seattle Biological Laboratory of the U.S. Bureau of Commercial Fisheries for making available data on albacore catches taken during offshore salmon gillnetting.

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Seasonal Fishing Quality Provided by the Natural Reproduction of Speckled Trout in Three Ontario Ponds¹

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ABSTRACT

A study was made of semi-monthly speckled trout catches from three similar ponds during the 5 fishing seasons for the 1956 to 1960 period. A catch totalling 15,088 trout and taken by 3,696 rod-hours was analyzed. Above-average catches of 2.9 undersized and 3.3 keeper trout per rod-hour occurred during the May 1-15 interval when the trout were particularly susceptible to angling. After this time, semi-monthly catches, composed of approximately equal numbers of undersized and keeper trout, averaged 3.8 trout per rod-hour. Except for the May 1-15 interval, variations in the levels of semi-monthly catches were found to result from differences in fishing intensity rather than from significant changes in the availability of trout. Annual natural reproduction and the continuous recruitment of young fish into the size group vulnerable to angling, therefore, maintained a standing population of trout at a level adequate to provide stability in the quality of angling throughout the fishing season.

INTRODUCTION

FISHING RECORDS provided by the Glen Major Fishing Club afford the opportunity to study the relationship of the size of trout catches to the time of year, fishing intensity, and the availability of trout in three ponds fished exclusively by its members. An analysis has been made of the daily angling and catch statistics kept by members for the 5 year period extending from 1956 to 1960. The method of angling was restricted to fly casting only. For the purpose of this paper, the the May 1st to September 15th open trout season has been divided into 9 semi-monthly intervals.

The ponds, located in agricultural southern Ontario at Lat. 44°N and Long. 79°W are very similar in limnological features. Each is slightly less than 2 acres (0.6-0.8 ha) in surface area with a maximum depth of about 9 feet (3 m), and is abundantly supplied with cold water and beds of *Chara*. Each of the ponds is fed by a spring creek providing excellent conditions for the natural reproduction of speckled trout, *Salvelinus fontinalis*, on which angling was dependent. The reader is referred to Ricker (1932) and McCrimmon and Berst (1961) for detailed descriptions of the ponds and their fisheries dating back to 1895.

The cooperation of A. M. Wilson, President, and members of the Glen Major Fishing Club in providing data necessary for the study is gratefully acknowledged.

¹Received for publication June 12, 1961.

TABLE I. Total catch of trout for the 1956-1960 fishing seasons.

Period	Catch of trout											
	Pond A			Pond B			Pond C			Composite, 3 ponds		
	Rod-hours of fishing	No. less than 7" over	No. 7" and over	Rod-hours of fishing	No. less than 7" over	No. 7" and over	Rod-hours of fishing	No. less than 7" over	No. 7" and over	Rod-hours of fishing	No. less than 7" over	No. 7" and over
May 1-15	164	359	544	128	348	459	133	519	402	425	1226	1405
May 16-31	176	371	292	119	323	219	117	344	242	412	1038	753
June 1-15	212	351	388	119	236	210	160	432	234	491	1019	832
June 16-30	161	273	279	95	186	168	109	310	158	365	769	605
July 1-15	142	249	295	98	113	125	133	271	199	373	633	619
July 16-31	136	275	335	128	252	278	116	256	193	380	783	806
Aug. 1-15	128	221	350	82	102	125	107	139	141	317	462	616
Aug. 16-31	198	310	421	135	255	282	150	266	253	483	831	956
Sept. 1-15	180	325	404	111	206	233	159	313	254	450	844	891
May 1-Sept. 15	1497	2734	3308	1015	2021	2099	1184	2850	2076	3696	7605	7483

FISHING INTENSITY

During the 5 year period from 1956 to 1960, the 3 ponds provided a total of 3,696 rod-hours of angling (Table I). Each of the ponds was fished for an average of 71–75 days each season at a level averaging 3.3 rod-hours per day. The maximum daily fishing pressure exerted on any of the ponds was 21 rod-hours, and daily angling rarely exceeded 10 rod-hours per pond.

Each of the ponds was subjected to similar total fishing intensities over the 5 year period, ranging from 1,015 rod-hours in Pond B to 1,497 rod-hours in Pond A. Fishing was distributed uniformly over the season when analyzed on a semi-monthly basis, reaching a low of 22.9% of the semi-monthly seasonal average of 411 rod-hours during the first half of August.

CATCH STATISTICS

A total catch of 15,088 trout was reported for the ponds during the 5 year period. This included 7,483 trout 7 inches (178 mm) or more in total length (to the tip of the tail when squeezed to maximum extension) which were mostly retained, and 7,605 trout of less than 7 inches which were returned to the water (Table I). The 7-inch length limit on keeper trout was a Provincial regulation discontinued after the 1959 season but retained by the Club for the purpose of this study. Keeper trout ranged upward from 7 inches and seldom exceeded 12 inches (305 mm) in length. Undersized trout in the catch were normally from 5 to 7 inches (127–178 mm) in length and the catch statistics include an unknown number of recaptures in this length range. On account of the selectivity of the angling gear, few trout less than 5 inches in length were caught.

KEEPER TROUT

Total catches of keeper trout from each of the ponds ranged from 2,076 and 2,099 fish for ponds C and B, respectively, to 3,307 fish for Pond A (Table I). However, fishing intensity was highest also in Pond A and fishing success there, when expressed as catch per unit effort, and was only 10% higher than the average of 2.0 trout per rod-hour for the three ponds. A total annual harvest of 294 trout per acre (726 per hectare) from the 3 ponds was realized.

A comparison of the composite catch by semi-monthly intervals (Fig. 1) shows a substantially higher catch for the first interval (May 1–15) than for any subsequent interval. Semi-monthly angling success was 3.3 trout per rod-hour during the first interval, which was 65% above the season average. During the remaining 8 semi-monthly intervals, fishing success was remarkably stable, varying no more than 20% from the seasonal average of 2.0 trout per rod-hour. Fishing quality for keeper trout was consistently higher in each pond on opening day of the season, averaging 4.4 trout per rod-hour.

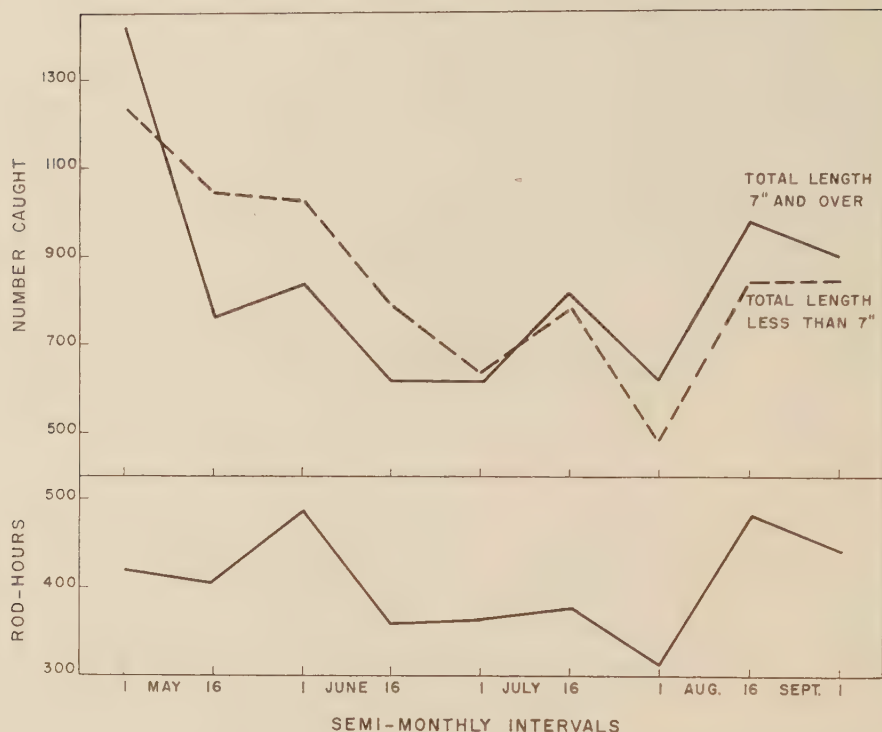


FIG. 1. Composite angling and catch statistics of the 3 ponds for the 1956-1960 fishing seasons.

UNDERSIZED TROUT

All trout measuring less than 7 inches and a few over 7 inches in total length were returned to the water and hence statistics include some recaptures. However, many of these undersized fish grew to become keeper trout during the angling season. Likewise, there was a continuous recruitment of smaller trout into that length range of undersized fish susceptible to the angler's hook.

Total catches of undersized trout from each of the ponds over the 5 year period (Table 1) ranged from 2,021 fish from Pond B to 2,734 and 2,850 fish from Ponds A and C, respectively. In spite of these differences in total catches, fishing success for small trout was actually very similar at 1.8, 2.0, and 2.1 trout per rod-hour for Ponds A, B, and C, respectively.

A comparison of combined catches from the 3 ponds on a semi-monthly basis during the fishing season (Fig. 1) shows the highest catch of undersized trout to have occurred within the period extending from May 1 to June 15 when 43.2% of the total catch was handled. The lowest catch was reported during the first half of August but was followed by higher catches in the latter half of August and September than had been realized since June.

A review of semi-monthly catches of undersized trout when expressed in relation to unit fishing effort reveals that the highest catches occurred during

May, after which time semi-monthly catches averaged about 1.9 fish per rod-hour over the remainder of the season. The optimum catch of undersized trout at 3.6 fish per rod-hour occurred on opening day of the fishing season.

SEASONAL FISHING QUALITY

From the semi-monthly composite catch per unit effort data plotted in Fig. 2, it is apparent that the quality of angling was highest at the beginning of the fishing season but dropped off by late May to a level of approximately 3.8 trout per rod-hour which was maintained for the remainder of the season. The shape of the curve approximates that for either undersized or keeper trout except that the actual curve for undersized trout is less steep in the semi-monthly intervals beginning on May 16 and June 1.

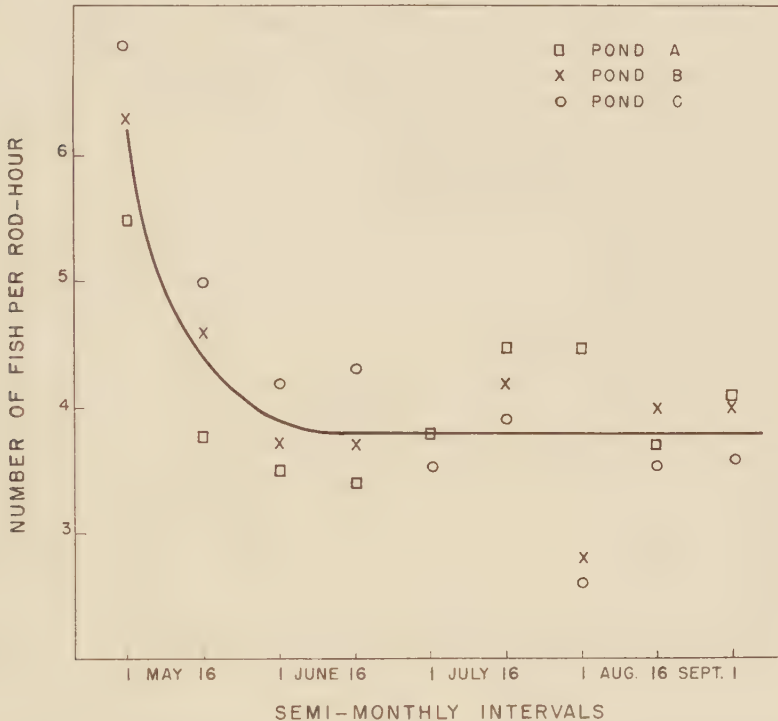


FIG. 2. Semi-monthly angling quality for the 3 ponds during the 1956-1960 fishing seasons.

The higher quality of angling at the beginning of the fishing season may be attributed to a build-up of trout in the length range susceptible to angling during the previous closed season and to the voracious appetite of the trout at that time of the year. The stability of angling quality through the summer months attests to the continuous recruitment of keeper trout from fish in the sub-keeper length range.

CONCLUSION

From the analysis of the 5 year fishing statistics for the 3 ponds, it may be concluded that natural reproduction and the continuous recruitment of smaller fish into the size group susceptible to angling was at least adequate to maintain the standing population of catchable trout at a level necessary to provide a consistent quality of angling throughout the fishing season. The correlation of fishing intensity with catch size through the season after mid-May is evidence of the availability of ample trout for angling of this intensity at all times.

Except for the above-average catches of trout during the May 1-15 interval when the fish are the most vulnerable to angling, variations recorded in the size of the catches for each of the semi-monthly intervals of the fishing season are a result of differences in fishing intensity rather than of significant changes in the availability of trout.

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Diving and Photographic Techniques for Observing and Recording Salmon Activities^{1,2}

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ABSTRACT

Techniques have been developed for underwater observation and photographic recording of salmon activities that are useful in various kinds of behaviour studies. Scuba divers can approach salmon sufficiently closely under some conditions to permit clear observation. From tests made both above the surface* and under water, an exposure chart has been prepared for salmon photography in rivers. Two examples are demonstrated. Colour film can be used, with appropriate filters, to render underwater objects in the colours they would have in air, or to give them untrue colours that assist in differentiating them from their background.

INTRODUCTION

FIELD STUDIES of salmon ecology and behaviour in rivers have long been hindered by two technical problems: how to observe salmon clearly and how to record their activities. The first problem can be partly solved by observing at the occasional favourable locality with calm, clear water, but a major breakthrough has recently come with the development of amateur scuba diving. In 1958 three of the Nanaimo Biological Station personnel, part of a group investigating the physiology and behaviour of salmon, were trained to dive, and since then have observed salmon in many previously inaccessible habitats (Fig. 1). The second problem has been tackled in part by developing photography as a recording technique. Most of the technical difficulties concerned have been overcome during two years' testing, 1959 and 1960. As a result the photography of salmon, both from above surface and under water, has taken its place as an effective research tool in the group's investigations. This paper describes the tests undertaken during the development of the photographic recording techniques, in particular those involving diving.

METHODS

Photographic equipment included a 6×6 Rolleiflex in Rolleimarin housing for underwater tests, a 35 mm Exakta for above surface photography, and a 16 mm Bell and Howell cine-camera in Sampson-Hall underwater housing. A Multiblitz Press electronic flash unit was used for above-surface recording at night. Little use was made of an underwater exposure meter, as surface turbulence prevented accurate and reliable readings.

¹Received for publication, May 16, 1961.

²Paper No. 4 concerning the physiology and behaviour of salmonid fishes from the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

Testing was mainly carried out at the Stamp and Sproat Rivers on Vancouver Island while based at the Fisheries Research Board field camp near Alberni.

The first tests in 1959 showed the necessity for reducing processing variation of film to a minimum. Consequently facilities were established to process black and white film at the field camp and the Biological Station, and arrangements were made with custom photofinishers to process colour and cine-film.

Two processing techniques were adopted for black and white roll film. The first was a field technique using Unibath 2 (Cormac Mfg. Co.) in a daylight loading tank. Fixed negatives were obtainable 8 minutes after shooting the final exposure. The second processing technique relied on Promicrol (May and Baker Ltd) as a one-shot developer using standard equipment and timing. Promicrol was selected as the single developer to be used throughout the tests with a variety of films, in view of its versatility and comprehensive instruction sheet. Developed film was cut into strips, contact printed (1 roll to an 8 × 10 sheet) and stored.

The following method was finally adopted for determining exposures in completely new situations. A roll of intermediate speed film (Kodak Plus X) was exposed with a range of 2 exposure values on either side of an estimate of the exposure. This film was developed (on the spot in Unibath if speed was essential) and the negatives examined to check correct exposure. If the particular photographic objective required a change of film emulsion, e.g., to colour, finer grain, faster speed, etc., appropriate exposure was calculated from the test roll, and the selected film then used.

Colour correction tests were undertaken to find means of restoring colours differentially absorbed by water. Three standard scenes in the Stamp River at depths of 2, 8 and 15 feet were selected and a series of 16 exposures taken at each depth using 5 densities of Kodak red, yellow and magenta filters plus a 0 filter control.

Tests with artificial light sources under water have so far been limited to still photography with No. 5 bulbs in Rolleimarin flash-holder. Series of bracketed exposures have been made of several scenes, with four emulsions at exposures calculated from manufacturer's guide numbers divided by the underwater light path (= twice focusing distance). Electronic flash has been used to obtain prints of nocturnal, surface-migrating fry and smolts. In these tests camera and flash were held, or mounted, vertically above the water surface.

During the tests little difficulty was found for scuba divers to approach salmon sufficiently closely for clear observation and for photography. Approach was easiest when many salmon were crowded together in small pools and subjected to strong currents. Under such conditions, salmon tended to ignore divers, particularly if they were approached stealthily from down-river and close to the bottom. However, it was almost impossible to approach adult salmon in open water, i.e., large pools and lakes. Sockeye were easier to approach than coho. Fry would come so close to quiet divers that the problem was to keep them sufficiently far away for focusing.

During the course of two summers a student assistant was trained to dive, and handle both the photography and processing whenever necessary.

The concept of "underwater light path" is important in calculating exposures for underwater photography, due to the rapid rate of absorption of light and underwater scattering (Schenck and Kendall, 1954). The underwater light path in natural light photography is the depth of the object plus the focusing distance. These are not completely interchangeable, however, in calculating exposures as scattering also limits the focusing distance by reducing definition. The maximum focusing distance for effective photography in the tested areas was 10 feet, even though salmon were usually visible at a distance of 20 to 30 feet in the clear river water.

For underwater exposure calculation, it is a considerable help to use the recently adopted A.S.A. Additive Speed Value system of film rating, and the Exposure Value (EV) system for light measurement, shutter speeds and apertures. However, the cameras used in these tests were calibrated in the traditional manner, as most photographic equipment still is, and so exposure data are presented in both systems. A conversion table is provided (Table I).

TABLE I. Conversion of Exposure Value (EV) system into terms of shutter speeds, apertures, film speeds and scene brightness.

Basic formula:							
Exposure value =		Time value +	Aperture value =		Speed value +	Brightness value	
Time value	Shutter speed	Aperture value	f/ stop	Speed value	ASA rating	Brightness value	Scene brightness ^a
	<i>sec</i>						<i>candles per sq. ft.</i>
0	1	0	f/1	0	3	0	0.352
1	1/2	1	f/1.4	1	6	1	0.704
2	1/4	2	f/2	2	12	2	1.41
3	1/8	3	f/2.8	3	25	3	2.82
4	1/15	4	f/4	4	50	4	5.63
5	1/30	5	f/5.6	5	100	5	11.3
6	1/60	6	f/8	6	200	6	22.5
7	1/125	7	f/11	7	400	7	45.1
8	1/250	8	f/16	8	800	8	90.1
9	1/500	9	f/22	9	1600	9	180
10	1/1000	10	f/32	10	3200	10	360
						11	721
						12	1442
						13	2884

^a Reflected light exposure meter reading off 18% reflectance card. Can also be measured as a light value in foot-candles by an incident light-meter.

RESULTS

Table II gives selected exposures for some scenes intensively photographed during the tests (Fig. 2-4). Fast shutter speeds and hence wide apertures were preferred in order to stop the normally rapid movements of salmon and water.

Such shutter speeds were usually possible in the tested area using medium speed black and white film to a maximum underwater light path of about 20 feet. The use of colour film was limited to very short underwater light paths of 12 feet or less, due to the need for colour correction by filters.

TABLE II. Effective underwater exposures in bright sun between 09:00 and 15:00 hours for the scenes most intensively photographed. *Film A*: Plus X. *Film B*: Superanscochrome daylight. *Film C*: HS Ektachrome daylight.

Scene	Underwater light path	Film	Filter	Exposure value	Shutter speed	Aperture
Fig. 2					<i>sec</i>	
Into water from above surface, with rock or gravel background	8 ft (=2× depth)	A	Polaroid	9.5	1/50	f/3.5
		B	Polaroid & CC30R	8.5	1/25	f/3.5
		C	Polaroid & CC30R	9	1/25	f/4.5
Fig. 3						
Under water, with plain background of water, rock, gravel or plants	5 ft	A	None	12.3	1/250	f/4.5
		B	CC30R	11	1/125	f/4.0
		C	CC30R	11.6	1/250	f/3.5
	12 ft	A	None	11.3	1/125	f/4.5
		B	CC50R	9.6	1/60	f/3.5
		C	CC50R	10.3	1/60	f/4.5
	20 ft	A	None	10.6	1/125	f/3.5
Fig. 4						
Under water, with white water background or surface	10 ft	A	None	13	1/500	f/4.0
		B	CC40R	12	1/250	f/4.0
		C	CC40R	12.6	1/500	f/3.5

Effective photography of salmon from above surface is limited by the need for polarising filters to eliminate surface glare (Fig. 2).

Table III shows colour correction filters selected for two underwater light paths using Superanscochrome daylight film. Even the usual minimum path, with object 3 feet from camera and both situated immediately below the surface, required a fairly strong filter (CC30R, or possibly CC20R) for satisfactory colour rendition. Interpolating into the table suggests a CC40R filter for an 8-foot underwater light path. Colour correction became almost impossible with an 18-foot underwater light path. Exposures with other colour films, Kodak

TABLE III. Colour correction filters required in Stamp River area.

Underwater light path	Correction filter
5 ft	CC30R
12 ft	CC50R
18 ft	Correction not practical

High-Speed Ektachrome and Anscochrome, both in daylight emulsions, suggested that different filter corrections might be necessary.

Correction for above-surface colour photography gave quite unnatural effects due to surface reflections, and hence would only be advisable if the reflections could be completely eliminated by polarising filters.

Results of test exposures of colour cine-film underwater showed that exposure calculations and colour correction established for 120 rolls of Superanscochrome daylight film could be applied without change to the same product in 16 mm cine-film. The test footage obtained has been made into a short movie demonstrating wandering movements of salmon schools in a turbulent pool, holding in a waterfall eddy, and deliberate selection of a narrow limited path through a calm and placid stretch of river.

Table IV shows effective underwater guide numbers for 4 films. These apply to shutter speeds of 1/500th sec and No. 5 clear bulbs. In general, flash photography is more suitable for recording young salmon (Fig. 5) than for adults, which are too large for even illumination at the short focusing distances imposed. The results showed little constancy in ratio between manufacturers' guide numbers and the effective underwater guide number. Hence, the latter cannot be accurately predicted, and need to be derived by the photographer for each film-flashbulb combination.

TABLE IV. Guide numbers for No. 5 clear flashbulbs at 1/500 sec in Rolleimarin 7-inch polished reflector.

Film	Manufacturers' Guide No. ^a	Underwater Guide No.
Black and white film		
Kodak Panatomic X	70	50
Adox R14	50	20
Colour film		
Anscochrome daylight	65	20
Kodacolor	65	15

^aBased on extrapolation from data supplied with flashbulbs.

Colour tests were made using clear bulbs and daylight film, which gave reasonable colour rendition without filtering through red adsorption by the water. However, colours could undoubtedly be improved. The use of blue bulbs was not satisfactory, as filtering was necessary for correct colour rendition, and they produced considerably less light than clear bulbs.

Nocturnal surface migrants can be photographed from above surface (Fig. 6) using electronic flash and normal guide numbers. By the use of high contrast, fine grain film in 35 mm camera, series of enlarged prints can be obtained demonstrating the direction of orientation of these migrants in relation to current direction.

CALCULATION OF EXPOSURE UNDER RIVER CONDITIONS

From these various tests a chart has been devised for calculating exposures within the testing rivers (Tables V, VI). Table V gives a basic above-surface Exposure Value taken from a Kodak, 18% reflectance, gray card. Table VI is a series of corrections to be made for weather, underwater light path, nature of background and filters. The basic exposure value depends in part on the processing techniques used. The factor "depth corrections" depends on turbidity, and consequently may vary from place to place and time to time. It should be checked frequently. The other factors should be constant within the period May-September, 09:00-15:00 hours.

TABLE V. Basic exposure values for three films, from light-meter reading of Kodak 18% reflectance gray card in bright sun 09:00-15:00 hours.

Film	Film speed	Exposure value	Shutter speed	Aperture
Plus X	5.5°	15	1/500	f/8
Superanscochrome daylight	5°	14.5	1/500	f/6.3
HS Ektachrome daylight	5.5°	15	1/500	f/8

TABLE VI. Chart for calculating underwater exposures in Stamp and Sproat Rivers. The "primary underwater correction" is for approximately 5 ft underwater light path. The "secondary correction" is minus 1 EV for each 7 ft of additional underwater light path.

Weather corrections		Basic exposure value (Table V)
Bright sun		
Cloudy bright		minus 1 EV
Cloudy dull		minus 2 EV
Heavy cloud		minus 3 EV
Primary underwater correction		minus 2.5 EV
Secondary underwater corrections		
12 ft underwater light path		minus 1 EV
20 ft underwater light path		minus 2 EV
Background corrections		
Much white water		plus 2 EV
Some white water		plus 1 EV
Open water		No correction
Unshaded background		No correction
Light shade		minus 1 EV
Much shade		minus 2 EV
Filter corrections		
CC20R		minus 0.5 EV
CC30R		minus 0.8 EV
CC40R		minus 1.1 EV
CC50R		minus 1.5 EV
Polaroid		minus 1.5 EV



FIG. 1. Scuba diver (D. V. Ellis) making cine-photographic recordings of the activities of a group of sockeye salmon holding in a waterfall eddy. Plus X film, bright sun, depth 3 feet, focusing distance 5 ft, some white water, turbulent surface, rock background with shadows, Exposure Value 13, 1/500 sec, f/4.0. Photograph by R. J. F. Smith.

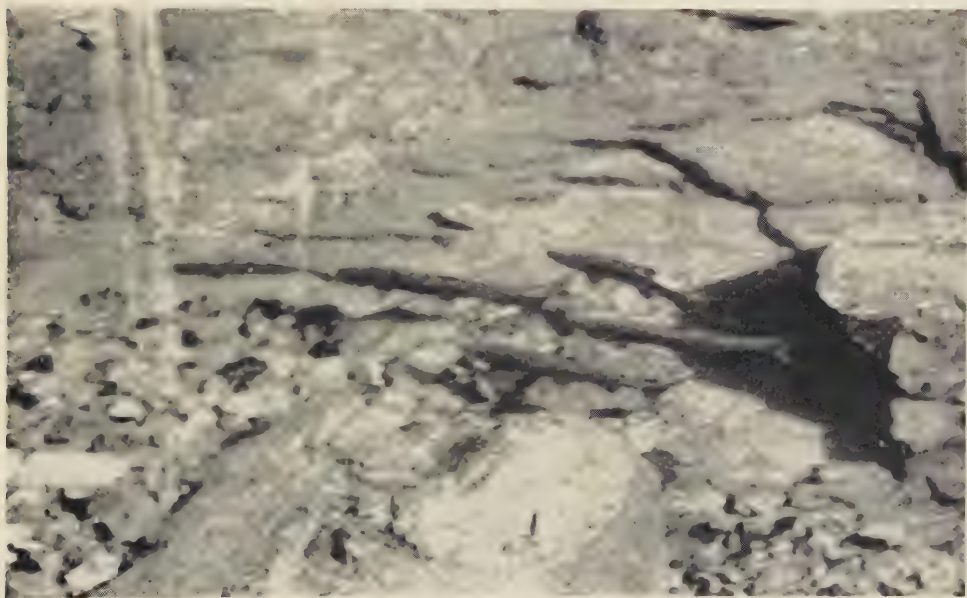


FIG. 2. A group of sockeye salmon picking their way slowly upriver. Photographed from above the surface. Plus X film, bright sun, depth 4 feet (underwater light path 8 feet = $2 \times$ depth), water surface calm, rock background, polaroid filter, Exposure Value 9.5, 1/50 sec, f/3.5.



FIG. 3. School of sockeye salmon wandering in a turbulent pool. Improved Tri-X film, bright sun, depth 6 feet, focusing distance 5 feet, surface slightly turbulent, rock background, Exposure Value 13.5, 1/500 sec, f/4.5.

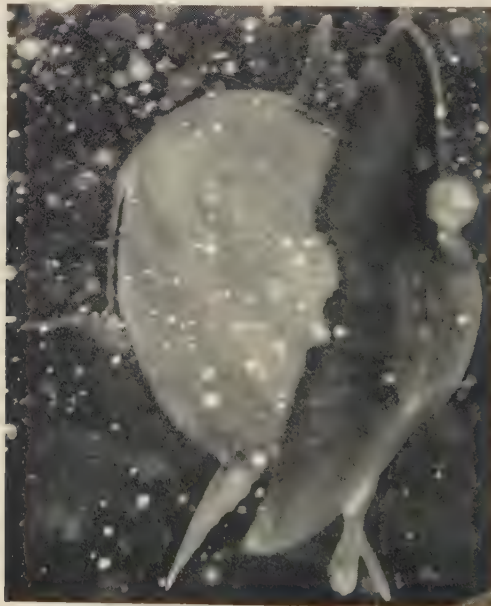


FIG. 4. Sockeye salmon amongst air bubbles from falling water. Plus X film, cloudy dull weather, depth 3 feet, focusing distance 4 feet, much white water, turbulent surface, rock background, Exposure Value 12.5, 1/500 sec, f/3.5.



FIG. 5. Part of a loose school of mixed 6-month-old coho fingerlings and young trout. Adox R14 film, No. 5 flashbulb, GN 20, focusing distance 4 feet, Exposure 1/500 sec, $f/5.0$.



FIG. 6. Sockeye smolts migrating downriver close to surface at night, over about 6 feet water depth. Camera held pointing vertically downward over side of anchored boat. Plus X film, Multiblitz Press flash unit, GN 50, focusing distance 6 feet, exposure 1/50 sec, $f/8$.

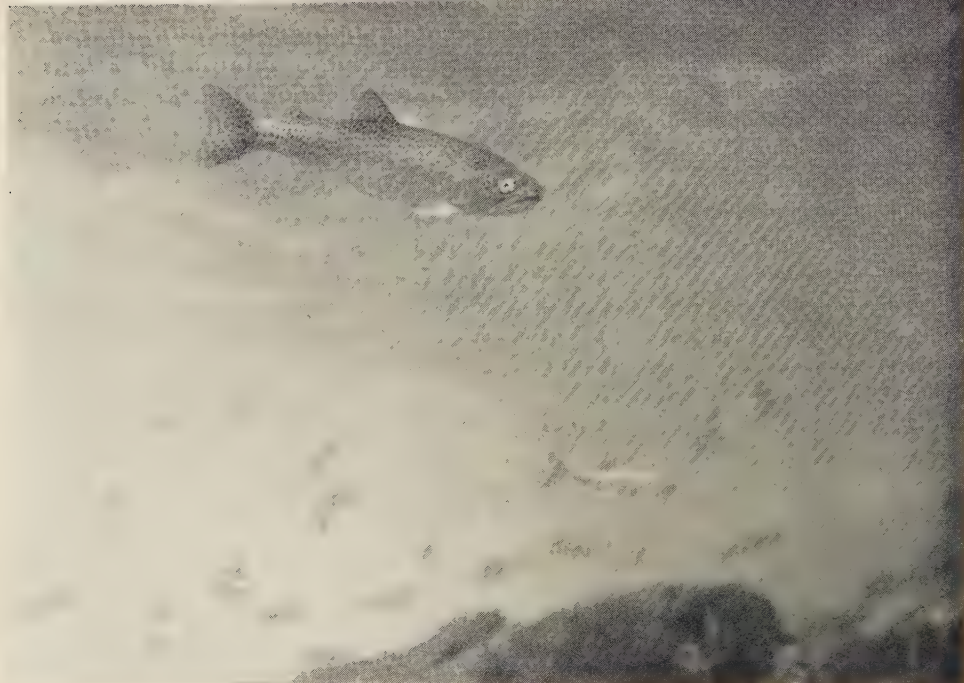


FIG. 7. Mixed group of young trout and coho fingerlings feeding in a waterfall eddy at the edge of the white water. Plus X film, bright sun, depth 3 feet, focusing distance 3 feet, white water background, turbulent surface, yellow filter (factor = minus 1 EV), Exposure Value 13.5, 1/500 sec, f/4.5.



FIG. 8. Adult sockeye holding at the edge of white water. The streamlined shape and clear, silvery scales demonstrate the appearance of early-run sockeye before change to spawning form. Black and white print from Superanscochrome (daylight) colour transparency, bright sun, depth 5 feet, focusing distance 5 feet, turbulent surface, white water background, CC40R filter, Exposure Value 12.5, 1/500 sec, f/3.5.

Exposures calculated from this chart agree to within 0.5 EV of data given in Table II. The chart has been used to check exposures for each photographic project in the better known situations, and as a guide to exposing a test roll of 120 black and white film in new situations. Two examples will be given to demonstrate its use.

Figure 2 illustrates a common problem in photographing salmon; that of recording them from above surface as they swim through calm, shallow water. For the sake of demonstrating exposure calculation the basic data will be changed from that quoted with the photograph. Given cloudy dull weather, maximum depth of 5 feet (= 10 feet underwater light path), and use Royal X Pan film at 9° film speed and a Polaroid filter, the exposure calculation is as follows:

Basic exposure in bright sun	EV 19
Corrections	
Weather (cloudy dull)	Minus 2
Primary underwater	Minus 2.5
Depth (10 ft ULP)	Minus 1
Background (unshaded bottom)	No correction
Filter (Polaroid)	Minus 1.5
Total corrections	Minus 7 EV
Calculated exposure	EV 19-7=EV 12, 1/250 sec, f/4.0

Figure 1 represents a far more difficult problem, due to surface turbulence causing great light fluctuations. Given basic data of 4 feet focusing distance and 3 feet depth, cloudy bright weather, and use of Superanscochrome daylight film for 16 mm cine-recording, then exposure calculation is as follows:

Basic exposure in bright sun	EV 14.5
Corrections	
Weather	Minus 1
Primary underwater	Minus 2.5
Depth (7 ft ULP)	Minus 0.5
Background (some white water)	Plus 1
Filter (7 ft ULP=CC30R)	Minus 0.8
Total corrections	Minus 3.8 EV
Calculated exposure at 24 f.p.s.	EV 14.5-3.8=EV 10.7, 1/50 sec, f/5.6

SIGNIFICANCE OF COLOUR FILM IN RECORDING

In general, colour photographic records are more easily interpreted than black and white, due to the low tonal range of the underwater world. However, below about 20 feet depth, colours become a monochromatic green (or blue). As a result, in deep water and using natural light, colour film loses its special advantages over black and white for research work. It still has legitimate uses, of course, for documentation and illustration.

Nevertheless, colour film can be used to show colours which exist underwater but are not visible to a diver due to the differential absorption of light. The standard ways of doing this at present are by the various techniques of artificial

lighting devised by Rebikoff, Cousteau, Hass, etc. Such artificial lighting introduces seriously disturbing factors, and at present seems of little use for cine-recording any range of animal behaviour, although it has its functions in still photography for ecological or morphological studies.

There are, fortunately, ways of correcting natural light in shallow water by means of filters differentially absorbing colours complementary to those absorbed by water. It is for this reason that colour correction tests have been undertaken here. The technique can be used to produce colours on film equivalent to those we would see were the fish swimming in air, for instance. Such added colour is a great aid to perception of the film image, and hence of considerable value as a tool for increasing the ease of analysing photographic records. As the correction filters remove much of the light, the technique can only be used effectively in shallow water—about 12 feet depth in the Somass system. It should not be forgotten though that the use of this technique produces colours on film which may have no visual significance to the species concerned. Indeed, it is even possible by the manipulation of filters to produce completely unnatural but vividly contrasting colours, which are of value through increasing the visibility of the photographed object against its background.

SUMMARY OF THE USES OF PHOTOGRAPHY AS A RECORDING MEDIUM

It is now possible to utilize photographic recording methods in field studies of salmon ecology and behaviour. In particular, cine-photography has value in recording salmon movements under turbulent or restricted conditions where note-writing by divers is impossible. Cine-photography is also useful for slow-motion recording of rapid movements such as jumping, attacking, etc., thus permitting detailed analysis of the sequence of events, and for sequence recording of simultaneous movements of schooling migrants.

Still photography permits obtaining enlarged prints on which to base descriptions of underwater environments, particular habitats selected by salmon and also trout (Fig. 7), the orientation of salmon and their seasonal morphological changes (Fig. 8). Photographs also provide means of illustrating these aspects of salmon biology as well as many others, e.g., social behaviour, feeding, etc.

ACKNOWLEDGMENTS

I am grateful to student assistant Mr R. J. F. Smith for his help with diving, photography and processing, to Messrs C. Shoop and C. Groot for occasionally acting as companion divers, and to the latter also for advice on photography.

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NOTES

Additional Records of the Argentinid Fish, *Leuroglossus stilbius* Gilbert, from British Columbia, with Remarks on its Taxonomy

Leuroglossus stilbius is a representative of the family Argentinidae, commonly referred to as deep-sea smelts. In describing the synonymy and distribution of this species from the North Pacific, Cohen (1956) examined many specimens from localities to the north and south of British Columbia. Only a single specimen, from off Five Finger Island, Strait of Georgia, was listed and this constituted the first record of the species from British Columbia.

Recently 12 additional specimens were caught in bottom trawls having fine mesh codends, during experimental shrimp fishing conducted aboard the Fisheries Research Board's vessel *Investigator No. 1*. Three were collected from a depth of 139 fathoms between Bowen and Gambier Islands in Howe Sound on November 17, 1960. Eight more specimens were taken from the same locality on June 8, 1961. A single fish was caught off the Middle Arm of the Fraser River at a depth of 90 fathoms on March 23, 1961¹.

Table I shows the fin ray counts and body measurements of these 11 specimens. Following Cohen's procedure, the last 3 lines of the Table show head length and body depth as percentages of standard length, and length of snout as percentage of head length. The values supplement Cohen's data, which deal with the entire known range of *L. stilbius* from the Okhotsk and Bering Seas to Central America.

Rass (1955, p. 329) divided *L. stilbius* into two subspecies. He considered the population inhabiting northern waters a distinct form, *L. stilbius schmidtii*, because there was no overlapping in the range of measurements of the 3 characters above with specimens from southern waters. However, data presented by Cohen showed that southern specimens had a wider variation than previously recorded. In the comparison below our calculated percentages (from Table I) fall within the ranges found by Cohen and appear to support his contention that there is little reason to recognize subspecies in *L. stilbius*.

Source	Body depth	Head length	Snout length
	%	%	%
Howe Sound, B.C.	15.8-18.7	28.1-34.1	24.0-31.0
Rass, 1955	13.3-16.5	25.4-31.0	28.4-33.8
Cohen, 1956	15.2-20.6	27.9-33.7	24.0-30.4

¹More specimens were caught in Howe Sound, at the above locality on August 24, 1961, and north of Woodfibre at 97 to 107 fathoms a day later; and off Crofton in Stuart Channel, east coast of Vancouver Island, at 110 fathoms on November 6, 1961.

TABLE I. Meristic counts and measurements of *Leuroglossus stilbius* from British Columbia.

Specimen No.	Howe Sound												Off Fraser R. Mar. 23, 1961 12
	November 17, 1960			June 8, 1961									
	1	2	3	4	5	6	7	8	9	10	11		
Dorsal rays	10	10	10	9	10	9	10	10	10	10	10	10	
Anal rays	13	12	12	12	13	12	13	13	12	13	13	...	
Pectoral rays	8	9	9	9, 8	9	9	8	9	9	9	8, 9	9	
Ventral rays	9	9	9	9	9	9	9	9	8, 9	9	9	9	
Standard length, mm	48.0	50.0	62.0	38.0	41.0	41.0	41.5	44.0	59.0	72.0	89.0	...	
Head length, mm	16.0	16.0	19.5	12.5	14.0	14.0	14.0	14.5	18.5	20.5	25.0	20.5	
Snout length, mm	4.0	4.6	5.5	3.0	3.5	3.7	4.0	4.5	5.0	5.5	7.0	6.0	
Eye diameter, mm	5.0	5.0	5.5	3.5	4.5	4.5	4.5	4.5	5.5	6.5	7.0	6.5	
Predorsal length, mm	27.0	28.0	35.0	22.5	24.5	24.5	25.0	26.5	34.5	38.5	51.0	39.0	
Prenasal length, mm	37.0	38.0	47.0	29.5	32.5	31.0	33.0	35.0	46.0	56.0	72.0	...	
Body depth, mm	9.0	9.0	10.5	6.0	7.5	7.5	7.5	7.5	10.5	12.0	15.0	12.0	
Head ÷ st. length, %	33.0	32.0	31.5	32.9	34.1	34.1	33.8	33.0	31.4	28.5	28.1	...	
Body depth ÷ st. length, %	18.7	18.0	16.9	15.8	18.3	18.3	18.1	17.0	17.8	16.7	16.9	...	
Snout ÷ head length, %	25.0	25.3	28.2	24.0	25.0	26.4	28.6	31.0	27.0	26.9	28.0	29.3	

Specimens are deposited in the National Museum, Ottawa, and the museum of the Institute of Fisheries at the University of British Columbia.

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

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Received for publication July 6, 1961.

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